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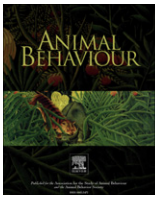

Exploratory behaviour of colonizing rats in novel environments

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The immediate movement and behaviour of individuals arriving in novel environments influence long-term survival and population establishment. Studies have previously investigated exploratory behaviour in novel laboratory environments, but never during colonization of natural systems. Experimentally releasing and monitoring animals would allow testing of laboratory and computer-simulation hypotheses. We sequentially released and tracked three adult male brown rats, *Rattus norvegicus*, on a rat-free island, monitoring their movements hourly for 3 weeks to test laboratory and simulation-generated hypotheses of how animals explore and move in novel environments. We found that (1) individual movements are apparently random; (2) range size increases most rapidly in the first week after arrival; (3) range size is larger than for individuals at high density; (4) movement is mediated by central place foraging behaviour. These findings contradict laboratory hypotheses of nonrandom exploration but support simulation search strategy hypotheses. Random movement and increased ranges at low density have implications for understanding animal colonization dynamics and intercepting invasive species arriving at new locations.

The movement and behaviour of first colonists in novel environments have important implications for their survival and long-term population establishment (Russell 1983; Holway & Suarez 1999; Taylor & Hastings 2005). Individuals in unfamiliar locations must become familiar with their environment before establishing home ranges (Russell 1983), allowing efficient resource utilization and predator avoidance (Birke & Archer 1983; Benhamou 1994; Burns 2005). Invasive species continue to colonize new environments (Vitousek et al. 1997), and preventing new invasions is a priority (Puth & Post 2005). Detecting and intercepting the first invaders remains difficult because of behavioural changes at low density such as enhanced neophobia (e.g. Thorsen et al. 2000), and a better understanding of invader behaviour would assist managers in preventing invasions (Holway & Suarez 1999; Puth & Post 2005).

Laboratory studies of exploration in novel environments hypothesize that animals will (i) initially prioritize a systematic exploration (avoiding sites previously visited) and (ii) subsequently settle into regular patterns of patrolling (regularly visiting previously used sites) about a home range (Birke & Archer 1983; Cowan 1983; Russell 1983). Computer simulations hypothesize that released individuals (iii) first explore around and return to their release site, before establishing new den sites about which they forage (Bovet & Bovet 1993), and (iv) choose nearly uncorrelated random-walk search strategies in the absence of specific cues in a homogeneous landscape (Zollner & Lima 1999).

Unfortunately, there is a lack of data outside the laboratory on animal behaviour in novel environments (Birke & Archer 1983; Gosling 2001) and on behavioural changes that occur following relocation from high- to low-density populations and familiar to novel environments (Smith & Morrell 2007). Such data are notoriously difficult to collect in natural systems, almost exclusively requiring an experimental approach (e.g. Burns 2005). Nonetheless, characterization of postarrival movement and behaviour is critical for understanding processes of species dispersal and colonization (Puth & Post 2005), and results from field experiments would provide a meaningful test of hypotheses developed in the laboratory (i and ii) and by computer simulation (iii and iv).

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We released single individuals of the invasive brown rat, *Rattus norvegicus*, on an island from which the species had been previously eradicated, as an experiment in invasion biology (Puth & Post 2005). Brown rats were used because they are a model species for laboratory studies and are also a widespread invasive species (Towns et al. 2006). Specifically, we looked for a change in movement and exploration consistent with a shift from hypothesized (1) systematic exploration to (2) range-based patrolling and from (3) den site establishment to (4) random search strategies.

METHODS

Five adult male brown rats (265–383 g) were individually released onto mammal-free Motuhoropapa Island (9.5 ha), New Zealand, over the summers of 2004–2005 and 2005–2006. Motuhoropapa Island has homogeneous forested habitat (Cameron 1998) and was selected because of its history of brown rat reinvasion (Clout & Russell 2006) and hence already marginalized flora and fauna. The release site for all rats was the only landing site on the western beach of the island. Each rat was captured and removed before the next release, and the island was left free of rats for 1 month between periods of behavioural observation to allow scent to dissipate. Adult male rats were used because they are not subject to hormonal behavioural changes from oestrus (Cowan 1983), roam more widely than females (Stroud 1982), and cannot become pregnant. Rats were captured from a high-density population on nearby uninhabited Pakihi Island (114 ha). All captured rats were anaesthetized with isoflurane, morphologically measured, and visually assessed for health. If suitable for transfer (healthy adult male), a 6 g (1.6–2.3% of rat body weight) single-stage brass loop collar radiotransmitter with internal aerial and thermoresistor mortality sensor (Biotrack U.K., Dorset) was attached, and a 1 mm tail sample was taken for genetic fingerprinting. Rats were then held for 48 h with food and water ad libitum in metallic wire cages (30 × 20 × 20 cm) prior to release on Motuhoropapa Island. Being a pest species in New Zealand, surplus rats were killed by cervical dislocation and disposed of. All work was performed under University of Auckland Animal Ethics permit R171.

Rats were located hourly during the first and third weeks postrelease from dusk until dawn and once daily in den sites by radiotelemetry triangulation. The rats were not approached closer than 10 m. Three bearings to the nearest 5° were taken within an average of 5 min of one another. Animal locations were estimated as the centre of the triangulation. Location error comprised triangulation precision, estimated as the area of each error triangle and expressed as the radius of a circle of that area, and accuracy, independently calibrated from 30 known locations with 10 m GPS error (sensu Lee et al. 1985). When a location was visually or acoustically confirmed, error was arbitrarily set at 5 m. All calculations were done in R 2.4.0.

We expressed the area traversed each night as the ‘prevailing range’ (sensu Doncaster & Macdonald 1991), because colonizing animals would not have established home ranges. Prevailing ranges were estimated from the minimum convex polygon of the nine nightly locations and tenth consecutive daily den site location. The focal centre of each nightly range was estimated by the harmonic mean centre (Lair 1987). Turning angles and den orientation angles after each step were estimated. Potential differences among rats were assessed with analysis of variance. All calculations were done in Python 2.5.2.

We tested rat movements against a hierarchical null model for random movement (sensu Bovet & Benhamou 1988) consisting of 1000 simulations within a bounded polygon identical to the island coast (sensu Jeanson et al. 2003). Because observed hourly rat movements were consistent across rats and weeks and did not differ significantly from an exponential distribution ($\lambda = 1/85$), and turning angles did not differ significantly from a uniform distribution (see Results), we simulated an uncorrelated random walk (i.e. Brownian motion). From each simulated location, starting at the release site, rats moved distance x drawn from an exponential distribution with scale parameter $\lambda = 1/85$ in a random direction (0–360°). If a simulated rat encountered the coast before completing its movement, it would continue traversing the coast until the total linear movement was equivalent to the original exponential draw. At the end of each night, simulated rats would either return directly to their previous den site or establish a new den site with probability θ_i on night i ($i = 1, \ldots, 21$) from our observed probabilities (see Results), where $\theta_i = 0.67$ for $i = 1, 2$; $\theta_i = 0.33$ for $i = 3$; and $\theta_i = 0$ for $i \geq 4$.

These simulations were used to generate null distribution parameters. The rate of simulated rat exploration of the island was summarized by the coefficients of the linear least-squares fit to the log-transformed cumulative range data. Log transformation linearized the cumulative range data. The intercept estimates expected range area after the first night, and the slope estimates the rate of island exploration. Average proportion of overlap in nightly range was calculated for simulated rats, providing an estimate of the level of patrolling (proportion of new range explored each night).

RESULTS

We triangulated 402 nightly locations and 44 den site locations. Radiotelemetry had a median precision of 5 m (SD = 10.31, $N = 325$) and accuracy of 14 m (SD = 9.10, $N = 30$). Three sequential bearings were taken within an average of 5 min (±5, $N = 397$) between first and last. There was no correlation between precision (spatial error) and time between bearings (temporal error; Spearman's rank correlation: $\rho = -0.09$, $P = 0.080$, $N = 360$), showing that rat movement between sequential bearings did not affect location precision. Sufficient data for statistical analyses were obtained for three rats. One rat destroyed its collar after 3 days and another died shortly after release. Rats ranged widely and eventually explored most of the island (Fig. 1).

The rats moved on average 85 ± 76 m (median = 59, $N = 354$) between hourly locations (Fig. 2a) and 685 ± 296 m ($N = 44$) every night. These estimates are minima as the animals were unlikely to have moved directly between locations. Individual hourly locations were treated as independent because a rat could potentially move anywhere on the island within an hour. No significant difference was detected in the hourly movement rates among rats (ANOVA: $F_{1,328} = 2.64$, $\beta = 0.79$, $P = 0.10$). Movement paths did not follow a Lévy flight, as step length was not linearly distributed according to a power law (cumulative distribution test, results not shown). Sizes of nightly prevailing ranges were highly variable and displayed no consistent pattern among the rats (Fig. 2b). Cumulative range size increased rapidly during the first week while the rats explored the island and stabilized by the third week, at which time full exploration of the island had been achieved (Fig. 2c). The rate of cumulative island exploration was highly predictable ($r > 0.90$, $P < 0.01$).

Turning angles were distributed widely (3 ± 115°; $N = 352$) and, despite some modality around 0 and ±180°, did not differ significantly from a uniform distribution (Kolmogorov–Smirnov test: $D = 0.07$, $P = 0.08$; Fig. 3a), but did differ significantly from a zero-centred Gaussian distribution (Kolmogorov–Smirnov test: $D = 0.16$, $P < 0.01$). The length of den site occupancy increased from only 1 night after release up to 6 or 7 consecutive nights during the third week, suggesting some stabilization. Turning orientation relative to

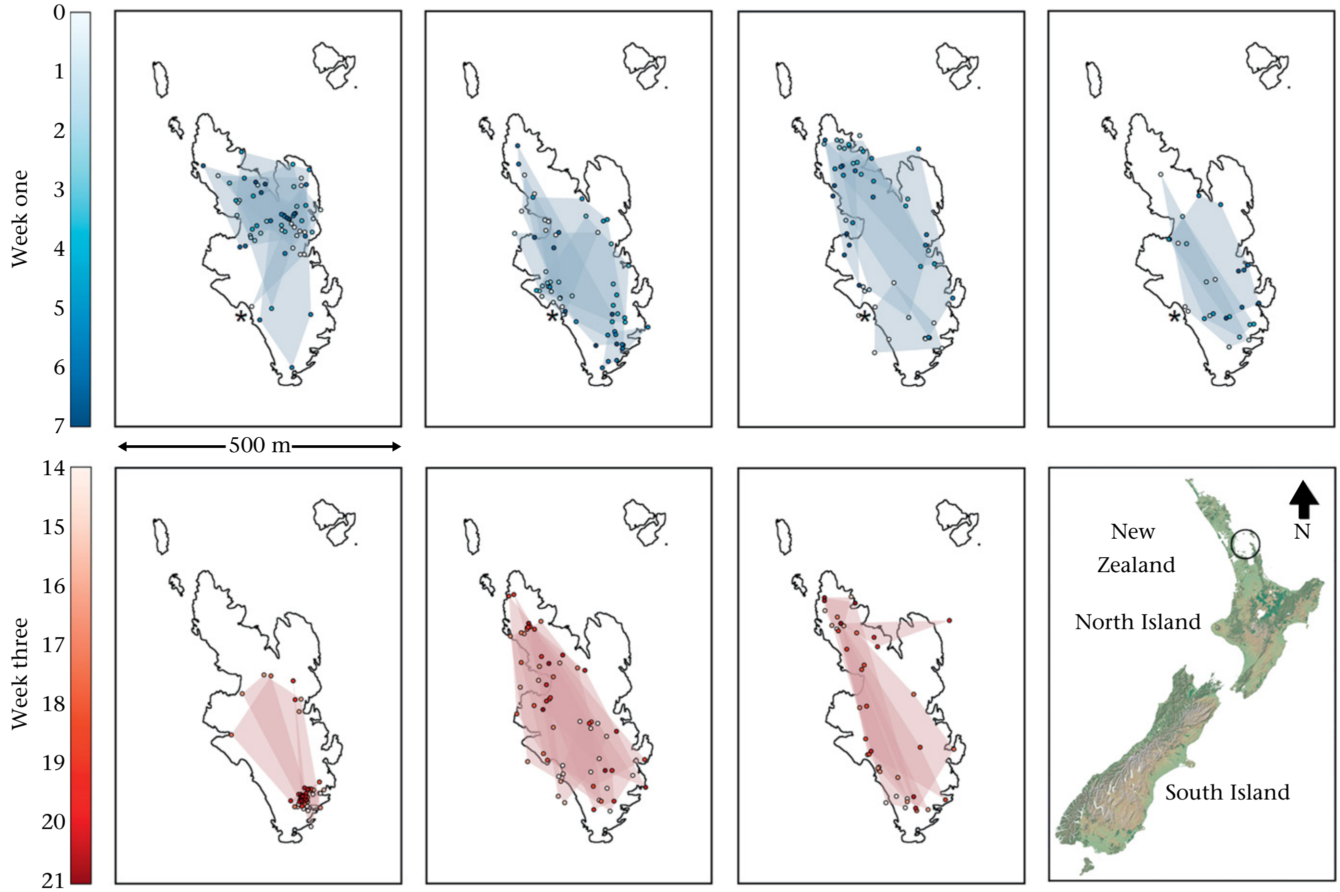

Figure 1. Radiotelemetry locations and nightly range minimum convex polygons (including den sites) of brown rats released on Motuhoropapa. The intensity of the shading indicates nightly prevailing range overlap. One rat lost its radiocollar during the first week (only first week shown); a second rat died upon release and is not shown. Asterisk indicates release site.

the previous den site (−3 ± 83°; $N = 385$) did not differ significantly from a zero-centred Gaussian distribution (Kolmogorov–Smirnov test: $D = 0.06$, $P = 0.17$; Fig. 3b), revealing that the rats oriented towards den sites. Nightly focal range centres were also constrained by den site locations, as each rat roamed from and around, and usually returned to, its most recent den site. The area explored on the first night, rate of island exploration, and patrolling behaviours were not significantly different from those of simulated rats moving randomly on an island in our null model (Fig. 4a–d).

DISCUSSION

Rats most rapidly increased their explored area of the island during the first week, in accordance with hypothesis (i), and by

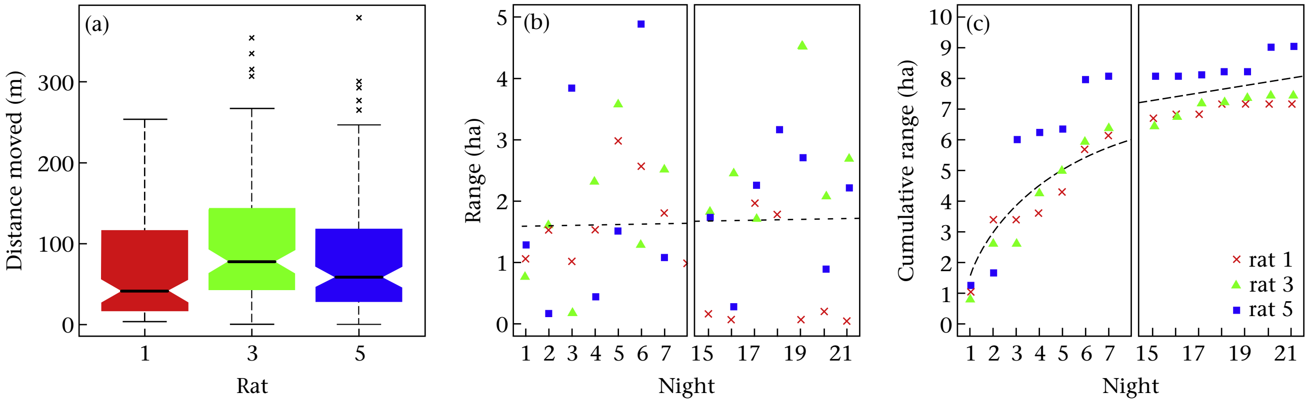

Figure 2. (a) Hourly movement box plot. (b) Nightly range sizes and (c) cumulative range sizes (including den sites) of single rats released on a mammal-free island and monitored for weeks 1 and 3 following release. Best-fit lines are least-squares linear (b; no significant trend, $r = 0.03$, $P = 0.83$) and logarithmic (c; significant trend, $r = 0.90$, $P < 0.01$).

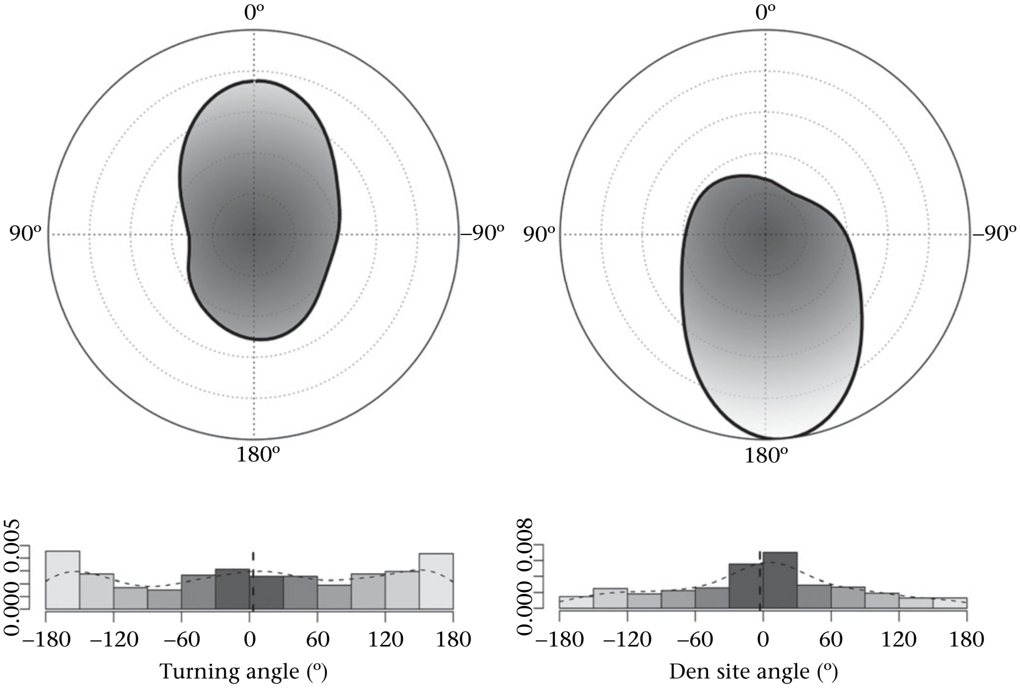

Figure 3. Circular and linear plots of (a) turning angles relative to the previous step ($N = 352$) and (b) turning angles relative to the previous den site ($N = 385$). Dotted lines are smoothed Gaussian kernel densities (bandwidth = 25).

week 3 had stable den sites about which they foraged, in accordance with hypothesis (ii). Total range explored increased over time as the rats increased their 'observation-area' curve. These findings superficially agree with hypothesized systematic exploration in novel environments, but could be generated by random movements alone, as our null model showed. The movements and area explored on any night by our individuals were apparently random, except the tendency to return to a previously used den site. Random movements alone generated an apparent pattern of 'patrolling' or 'spontaneous alternation' (Cowan 1983; Russell 1983), whereby rats would visit parts of their territory that had not been visited the previous night. Such random (Brownian) search patterns, moderated by return to a start site (i.e. the den), have also been observed in insects (Hoffmann 1983). Whereas in the laboratory rats may rapidly become familiar with restricted novel environments and move beyond random movement, this process may take much longer in natural environments with multiple complex cues that may take recently arrived individuals longer to assimilate before movement becomes nonrandom.

Central place foraging would lower the rate at which exploration occurs, but could enable rats to become familiar preferentially with locations closer to their den sites and reorient relative to their den site as required. Thus den sites played an important role in determining the range a rat would explore on any given night, in accordance with hypothesis (iii). Whether searching for a specific resource (e.g. food or conspecifics) or simply to enhance environmental information, the same general rules of search optimization apply. Our rats effectively followed a weakly correlated random walk, in accordance with hypothesis (iv), which depended most strongly on den site location, as computer simulations have hypothesized (Bovet & Bovet 1993; Zollner & Lima 1999).

At low densities home-range size has been alternatively predicted as either larger because of a lack of competitive interactions or smaller because of a lack of competition for resources (Jetz et al. 2004). At high densities brown rats are usually sedentary with home ranges around 1–2 ha (Recht 1982; Stroud 1982). After 3 weeks on the island the total range explored (the entire 9.5 ha island) was larger than the recorded home ranges of individuals in high-density populations monitored for similar time periods (Cowan et al. 2003; Innes 2005). Generally, animals are familiar with an area that is larger than the home range they occupy, with size of the home range being limited by energetic requirements and conspecific interactions (Cowan 1983). Previously, individual brown rats released into a high-density population remained within only 30 m of release (Calhoun 1948). In contrast, we found that brown rats with no conspecifics were more mobile, moving away from their release site and maintaining larger home ranges in a new environment, supporting the hypothesis that home-range size is limited by conspecific interactions. Mice released into novel environments in the absence of conspecifics also select higher quality home ranges (Burns 2005). Containment, similar to accidental transportation on vessels, is unlikely to have altered rat behaviour. In laboratory environments previous containment changes only the type of exploratory behaviour, rather than overall activity levels (Rosellini & Widman 1989), and affects rats only for the first few hours after release (Russell 1983).

Knowledge of how dispersing rats behave, and the size and location of their ranges over time, has implications for control strategies. Dispersal is positively correlated with exploration, and so dispersing animals are also those more likely to range widely when not dispersing (Dingemanse et al. 2003). Widely and unpredictably dispersing colonizing individuals would generate a behavioural Allee effect (Taylor & Hastings 2005), but continuously increasing range size could compensate by increasing the probability of encountering conspecifics. If colonists move and establish den sites randomly, and as an outcome have consistently increasing cumulative range sizes, then responses to suspected invasions must be rapid and increase the search area as time since arrival increases. Last, density-dependent changes in behaviour and movement patterns have implications not just for the detection and control of invading species, but also for the reintroduction of threatened species to new locations to maintain viable populations.

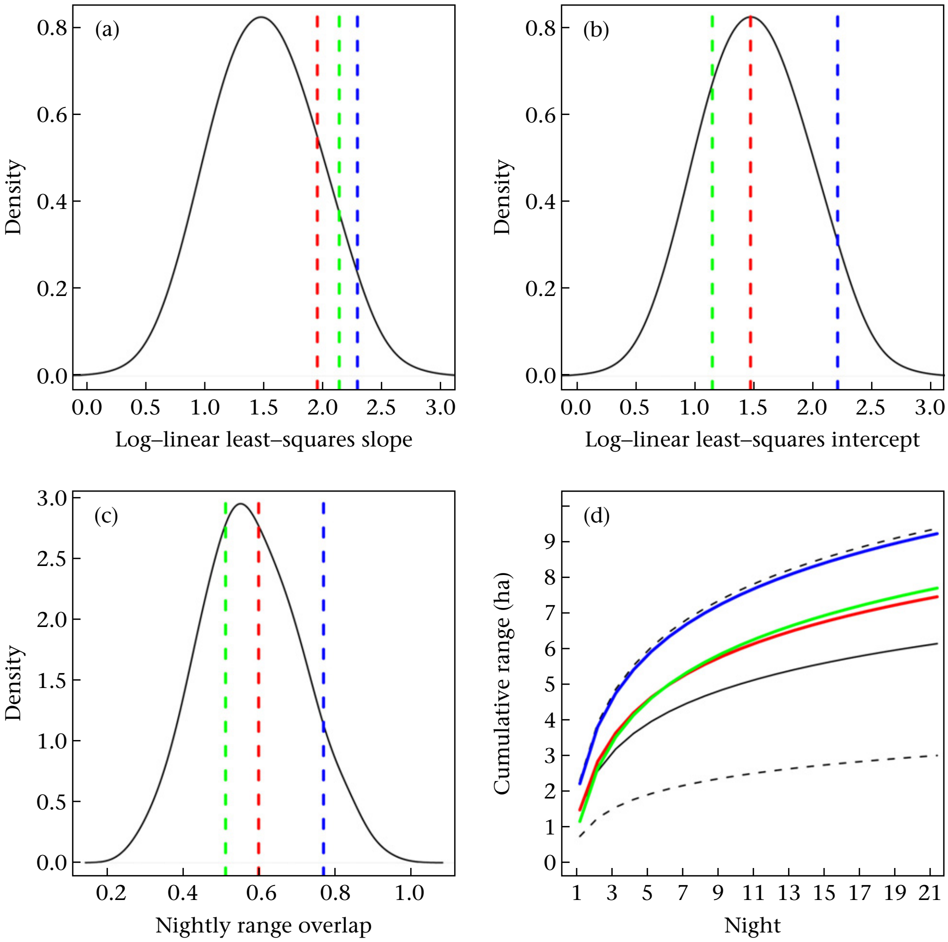

Figure 4. Null model results for $N = 1000$ randomly moving rats; lines indicate observed values for rats. (a) Distribution of the intercept (expected range size in hectares after the first night) using a log-linear least-squares fit to cumulative island area explored over 3 weeks. $P = 0.33$, 0.15, 0.06. (b) Distribution of the slope (rate of island exploration in hectares) using a log-linear least-squares fit to cumulative island area explored over 3 weeks. $P = 0.96$, 0.43, 0.10. (c) Distribution of the proportion of nightly range not patrolled the previous night. $P = 0.85$, 0.64, 0.15. (d) The expected rate of increase in nightly cumulative range (±95% confidence interval).

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