



Slow natal dispersal across a homogeneous landscape suggests the use of mixed movement behaviours during dispersal in the Darwin's frog

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Dispersal is a key process in ecology and evolution. Both theoretical and empirical evidence in actively dispersing organisms support the general notion that the use of nearly straight dispersal paths is a highly efficient way to maximize dispersal success in heterogeneous landscapes. In homogeneous landscapes, in contrast, the benefits of a straighter dispersal path could be outweighed by an increase in risk costs, favouring the evolution of tortuous dispersal paths resulting in a relatively slow dispersal. Empirical support for this theoretical prediction, however, has remained elusive. To explore this theoretical prediction, we studied the movement behaviour of the southern Darwin's frog, *Rhinoderma darwinii*, a fully terrestrial amphibian inhabiting a highly homogeneous environment (i.e. South American temperate forest). Using spatial capture–recapture data collected over a 4-year period in wild populations, in combination with statistical and simulation modelling, we found evidence of a slow natal dispersal lasting one year or more. In contrast, adults exhibited high site fidelity, having a median annual displacement of 3.64 m. A correlated random walk model produced synthetic distributions of juvenile annual displacement that were nearly identical to the empirical data, suggesting that a plausible explanation of juvenile dispersal is the use of routine movements (with high path tortuosity) over short temporal scales (<3 months) integrated over the year along a relatively straight dispersal path. We predict that for species living in homogeneous landscapes, this behaviour likely reduces many of the costs associated with the transient stage of dispersal. Specifically, periods of routine movements might reduce risk costs (e.g. dying due to starvation or predation), while the integration of these periods along a straight line maximizes dispersal distance while minimizing energetic costs.

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Although its drivers, mechanisms and consequences can vary enormously, movement from one spatial location to another is a

process inherent to almost every organism on Earth (Nathan et al., 2008). In general, animals move in space in order to (1) exploit resources (e.g. foraging, mate searching; i.e. routine movements), (2) maximize resource exploitation in environments with predictable spatiotemporal variation in ecological conditions (roundtrip movements known as 'migrations'), or (3) change from one natal or breeding site to another breeding site (i.e. dispersal) (Clobert, Le Gaillard, Cote, Meylan, & Massot, 2009; Matthysen, 2012; Van Dyck & Baguette, 2005). Importantly, these movement types have different ecological and evolutionary consequences. Notably, dispersal is a critical process with profound consequences for gene flow (Ronce, 2007) and which affects the dynamics of spatially

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structured populations (Revilla & Wiegand, 2008), species distribution ranges (Kokko & López-Sepulcre, 2006) and, ultimately, a species' ability to persist in stochastic or changing environments (Kokko & López-Sepulcre, 2006; Ronce, 2007; Schloss, Nuñez, & Lawler, 2012).

Foraging and other routine movements are generally characterized by a high level of returning and low net displacement as individuals stay within their home ranges, while dispersal-related movements are usually considered to be specialized, fast movements designed to enhance net displacement (Schtickzelle, Joiris, Vand Dyck, & Baguette, 2007; Van Dyck & Baguette, 2005). Both theoretical and empirical evidence support the general notion that the evolution of nearly straight dispersal paths is a highly efficient way to maximize dispersal success in heterogeneous landscapes (Bartoń et al., 2009, 2012; Brown, Phillips, & Shine, 2014; del Mar Delgado, Penteriani, Nams, & Campioni, 2009; Fahrig, 2007; Heinz & Strand, 2006; Palmer, Coulon, & Travis, 2011; Schtickzelle et al., 2007; Zollner & Lima, 1999), most likely because persistence in movement directionality enhances the chances of finding a suitable patch before dying in an inhospitable landscape matrix (Fahrig, 2007; Palmer et al., 2011; Zollner & Lima, 1999). In relatively homogeneous landscapes (i.e. landscapes with continuous or nearly continuous suitable habitat), in contrast, this benefit of a straighter dispersal path could be outweighed by an increase in risk costs (sensu Bonte et al., 2012; e.g. dying due to starvation or predation) associated with this type of movement (e.g. individuals could be more prone to predation). Indeed, individuals face a behavioural trade-off during dispersal: the use of straight and fast displacements is traded against the performance of movements with a more tortuous trajectory, such as those associated with foraging and predator avoidance (Bonte et al., 2012; Zollner & Lima, 2005). Thus, it has been hypothesized that in species that evolved in relatively homogeneous landscapes (or patchy landscapes with a low-risk matrix), the optimal movement path during dispersal should be tortuous as individuals are expected to display routine movement behaviours more often than would be expected to occur in a more patchy landscape (Fahrig, 2007; Van Dyck & Baguette, 2005). For a given distance, a more tortuous dispersal path should also increase dispersal duration. Yet, empirical support for these theoretical predictions has remained elusive due to a scarcity of data concerning the duration of, and movement trajectory during, dispersal in animals inhabiting homogeneous landscapes.

Amphibians are a diverse taxonomic group that exhibits different developmental modes associated with contrasting life history strategies (Müller et al., 2013). Amphibians with aquatic larvae (e.g. pond-breeding amphibians) usually require landscape complementation (Becker, Loyola, Haddad, & Zamudio, 2010). This means that individuals have to use both terrestrial and aquatic habitats; these are embedded within a risky landscape matrix that needs to be traversed during migration and dispersal (i.e. heterogeneous landscapes; Becker et al., 2010). In contrast, fully terrestrial amphibians (i.e. species with direct or indirect development in terrestrial environments) generally do not require landscape complementation for breeding or feeding (Becker et al., 2010). Consequently, they inhabit highly homogeneous landscapes (commonly forests with high humidity levels) where the terrestrialization of their breeding strategies has evolved (Müller et al., 2013). These animals show a remarkably low vagility and small home ranges (Wells, 2007). Therefore, fully terrestrial amphibians represent an interesting, although rarely explored, model to study patterns of dispersal duration and path trajectory in vertebrates that evolved in highly homogeneous landscapes.

In this work, we study the movement behaviour of the southern Darwin's frog, *Rhinoderma darwinii*, an endangered (IUCN 2018; <http://www.iucnredlist.org/details/19513/0>), small-sized (<5 g during adulthood), fully terrestrial frog inhabiting a highly homogeneous landscape (temperate forest of South America; Valenzuela-Sánchez, Cunningham, & Soto-Azat, 2015). To this end, we use spatial capture–recapture data collected over a 4-year period, in combination with statistical and simulation modelling. From a practical perspective, it could be particularly hard to determine the onset and end of dispersal events in animals using homogeneous landscapes with infrequent or unapparent habitat boundaries (Nathan, Klein, Robledo-Arnuncio, & Revilla, 2012). Based on dispersal ecology theory, the ultimate (evolutionary) drivers of dispersal in species using spatiotemporal homogeneous environments should be the avoidance of kin competition and/or inbreeding depression (Bowler & Benton, 2005; Johst & Brandl, 1999; Perrin & Goudet, 2001; Szulkin & Sheldon, 2008). Therefore, because moving away from the natal site before reaching adulthood should reduce kin competition and inbreeding more efficiently than afterwards, we expect natal dispersal (i.e. dispersing before first reproduction) to be more common than breeding dispersal (i.e. dispersing between two breeding attempts) in fully terrestrial amphibians. Consequently, even though the onset and end of dispersal cannot easily be defined in our study species, we expected to observe a divergence in movement behaviour between juveniles and adults, with juveniles more often presenting dispersal-related movement behaviour. Valenzuela-Sánchez, Harding, Cunningham, Chirgwin, and C Soto-Azat (2014) showed that adults and juveniles of this species have a similar movement behaviour over a 3-month period. Therefore, we predicted natal dispersal in this species to be the result of routine movements taking place over a relatively long temporal scale instead of being the result of fast movements lasting a few days (as could be expected for animals using highly heterogeneous landscapes). Specifically, we expected (1) juveniles and adults to exhibit similar displacement distributions over two short temporal scales (daily and 3-month displacements) but to differ over a longer temporal scale (annual displacement) and (2) the routine movements of juveniles to be integrated over the year along a nearly straight path. In species dispersing within homogeneous landscapes, this solution of mixed movement behaviours might reduce risk costs (e.g. dying due to starvation or predation) while maximizing dispersal distance and minimizing energetic costs.

METHODS

Study System

Between March 2014 and December 2017, we carried out a capture–recapture (CR) study in two rectangular plots (HUI1 and HUI2) with *R. darwinii* presence in the Reserva Biológica Huilo Huilo, Neltume, in southern Chile. These plots are located nearby (interplot distance: 4.5 km), both embedded within forest stands of >10 ha representing apparently continuous habitat for *R. darwinii*. This species is a forest specialist that is found only within native forest (Valenzuela-Sánchez et al., 2015). The abundance of the species is positively correlated with stand basal area (Valenzuela-Sánchez et al., 2019). Old-growth forests in this region are associated with high values of this structural attribute (Valenzuela-Sánchez et al., 2019). The structural complexity of old-growth forests buffers spatiotemporal environmental fluctuation, making these systems particularly homogeneous (Chen et al., 1999; Spies & Franklin, 1988). HUI1 and HUI2 are within old-growth forest stands

of similar composition and structure. Both plots exhibit a high stand basal area (>100 m²/ha), a low daily microclimatic fluctuation and high humidity (Valenzuela-Sánchez et al., 2019). Both forest stands are currently protected from logging activity because they are located within a private protected area. Genetic and capture–recapture evidence suggest that maximum dispersal distances are very short in fully terrestrial amphibians (generally <150 m; Smith & Green, 2005). Therefore, considering the common finding that the distribution of dispersal distances in a population tend to be highly leptokurtic and right skewed, the sizes of our study plots (HUI1 = 0.49 ha, HUI2 = 0.52 ha) are likely to capture a proportion of the *R. darwinii* dispersal events. Indeed, the maximum length of both study plots (i.e. diagonal of the rectangle) was ~100 m, which is 34 times longer than the average net displacement measured in juveniles and adults of the species over a 3-month period (2.95 m; Valenzuela-Sánchez et al., 2014).

Age-specific Spatial Capture–recapture Data

We collected search-encounter spatial CR data for two nested levels of capture occasions. At each plot, we carried out nine primary survey periods (sensu Pollock, 1982). Consecutive primary survey periods were separated by a 3-, 6-, 9- or 12-month interval (Fig. 1a). During each of these periods, we performed four secondary survey occasions, i.e. each plot was surveyed daily on 4 consecutive days by two fieldworkers for 2 h per day. Captured frogs were measured (snout-to-vent length, SVL), photographed for individual recognition using their ventral coloration patterns, and released at the exact point of capture (Valenzuela-Sánchez et al., 2017). Each capture location was mapped (x and y coordinates) with a ± 10 cm precision (Valenzuela-Sánchez et al., 2014). Details on searching, handling and mapping methodology are described elsewhere (Valenzuela-Sánchez et al., 2014, 2017). We assigned

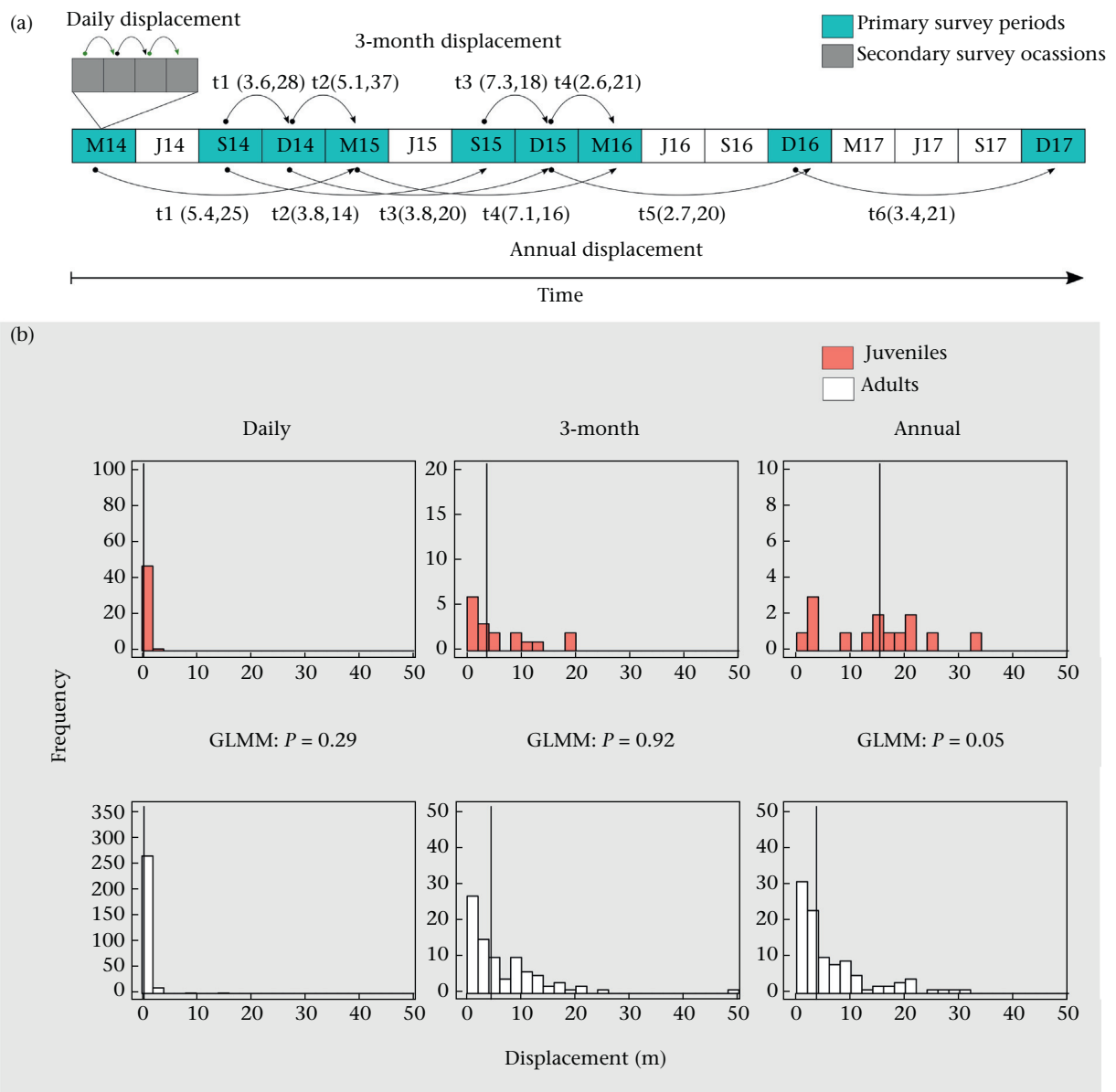


Figure 1. (a) Temporal configuration of the capture–recapture study of southern Darwin's frogs (*Rhinoderma darwinii*) showing the different time intervals (t1, t2, ... t_{total}) during which displacement data were obtained (median displacement in metres; total number of records displayed in parentheses). In (b), age-specific histograms of displacement at the three evaluated temporal scales are shown. The black vertical line indicates the median displacement. The capture–recapture of frogs was performed at two study sites in Neltume, southern Chile.

each captured frog to one of three age classes: recently metamorphosed (SVL < 11 mm), juvenile (SVL \geq 11 and \leq 24 mm) and adult (SVL > 24 mm). Recently metamorphosed frogs were rarely captured, and since their individual ventral marks were not completely developed, we did not include them in any analyses. Based on our field observations, the locomotor capacity (both jumping and endurance) of recently metamorphosed frogs is poorly developed, which should reduce the likelihood of observing dispersal-related behaviour during this age. Only individuals with SVL > 24 mm were observed as reproductively active, and this was based on morphological characteristics (i.e. presence of vocal sac in males and enlargement of the coelomic cavity in gravid females; Valenzuela-Sánchez et al., 2014). In our study populations, adulthood is reached, on average, at approximately 2 years of age (Valenzuela-Sánchez et al., 2017).

Observed Movements: Daily, 3-Month and Annual Displacement

As expected due to proximity and environmental similarity between HUI1 and HUI2, data exploration revealed no major differences in frog movements between plots. Therefore, we pooled data from both plots for subsequent analyses. Our spatial CR data allowed us to directly calculate displacements (i.e. Euclidean distance between two capture locations) at different temporal scales (Fig. 1b). Within each primary survey period we measured daily displacement, and between primary survey periods we calculated 3- and 12-month (annual) displacement. We compared displacements between juveniles and adults at the three temporal scales using a generalized linear mixed model of the gamma family (gamma GLMM), with individuals as a random effect, using the package 'lme4' (Bates, Maechler, Bolker, & Walker, 2015) in R v.3.4.4 (R Core Team, 2018). Based on Akaike's information criterion, AIC, other probability distributions (e.g. lognormal, Weibull, normal) did not provide a better fit to the displacement data.

Testing the Homogeneity of the Landscape

Our predictions about age-dependent dispersal, dispersal duration and the incorporation of routine movements along a nearly straight dispersal path in *R. darwinii* are all based on the assumption of a spatiotemporal homogeneous environment. In addition to the description of our study system, which suggests a high level of environmental homogeneity in space and time, we tested whether this assumption was reasonable based on the distribution of the polar direction (bearing angle) of the recorded annual displacements (due to a small sample size per plot, juveniles and adults were pooled for this analysis). In a spatially homogeneous landscape, one would expect to find uniformly distributed angles. The Rayleigh's test of uniformity for circular data was used to evaluate uniformity in bearing angles.

Estimated X- and Y-direction Movements

We used the spatial Cormack–Jolly–Seber model (sCJS model; Schaub & Royle, 2014) to estimate the distribution of 3-month frog displacements using our CR data, which have spatial locations stored in Cartesian coordinates. In this model, displacements are not directly estimated; instead, displacement variances in two directions (i.e. x- and y-direction movements) are estimated (for further details, see Schaub & Royle, 2014). Specifically, we used a scaled t distribution to describe the x- and y-direction movements at the 3-month scale. To this end, we pooled x- and y-direction movements and we estimated a single value for each t distribution parameter (i.e. degrees of freedom and scale) for each age class. These parameters were then used to simulate displacement at the

annual scale (see below). Further details on model construction and parameter estimation can be found in the Appendix.

Movement Path Model: Structure

We constructed a simulation model to describe the movement of single individuals in a two-dimensional, spatially continuous arena (movement path model, MP model). This model was specifically used to test the prediction that dispersing juveniles perform routine movements integrated over the year along a nearly straight path. The MP model is discrete in time, meaning that individuals move in discrete steps. During each step, individuals select the displacement (step length) and direction (turning angle) of the movement. The simulated landscape is completely homogeneous. Survival probability is held constant at 1. Step duration is 3 months, and the model runs during four consecutive steps. The Euclidean distance between the first and the last individual's spatial location represents an annual displacement. Importantly, individuals can follow one of three simple rules when they move: noncorrelated nonstationary random walks (NRW), correlated nonstationary random walks (CRW) or stationary random walks (SRW). The NRW and CRW are similar, both are modelled as a first-order Markovian process, where the location of an individual in time t depends on its spatial location at $t - 1$. For these random walks, we set up the turning angle by using a wrapped Cauchy circular distribution, which has a concentration parameter (r) that ranges from 0 (no correlation in movement directionality between steps, leading to a highly tortuous path) to 1 (absolute correlation in movement directionality between steps, leading to a fully straight path; Bartoń et al., 2009; Bartoń et al., 2012; Zollner & Lima, 1999). The NRW is unbiased, i.e. there is no preferred direction in each movement step (Codling, Plank, & Benhamou, 2008) and, therefore, r was fixed to 0. In contrast, the CRW includes persistence in movement directionality (Codling et al., 2008). In this case, we tested different degrees of persistence in movement directionality by testing different values of r that ranged from 0.1 to 1. Finally, the SRW assumes that individuals have an activity centre to which all their spatial locations are related. In the NRW, CRW and SRW, step length was drawn from a scaled t distribution using the R package metRology (Ellison, 2017) and parameter values were estimated using the sCJS model. As posited in the Introduction, we expected dispersing juveniles to follow a CRW with high r values (i.e. high movement directionality persistence) at the temporal scale and resolution evaluated here (i.e. 3-month steps coupled within a 1-year period). Note that at a shorter temporal scale, e.g. daily steps within a 3-month period, we expected dispersers to follow different movement rules, however, our empirical data suggest that these routine movements would hardly be predicted in this species using simple random walk models (Appendix, Table A2), probably because individuals change behavioural states continuously according to the nature of the movement (e.g. antipredatory versus feeding behaviour). Simulations were run using R v.3.4.4 (R Core Team, 2018).

Movement Path Model: Simulations and Performance

The simulation of our MP model variations started with two independent plots holding *R. darwinii* individuals (spatial locations, number and age of individuals equal to those observed at the first primary capture period in each plot: HUI1: $N = 60$; HUI2: $N = 29$; total juveniles: $N = 22$; total adults: $N = 67$). In the SRW, for a given individual, the activity centre is simply assumed to be its initial spatial location. Although individuals were free to move in a virtually infinite arena, we only sampled individuals that stayed within the area of the empirical plots. This provided model outputs with the presence of movement truncation (a source of observation

error in CR data; Schaub & Royle, 2014); these being directly comparable with the empirical data set. We ran 1000 simulations of each model variation. As with the empirical data set, displacements from the two simulated plots were pooled for analyses. We evaluated the performance of each model variation by following two criteria. First, during each simulation we estimated the mean and median of the simulated annual displacement of juveniles and adults, and compared these values with the empirical ones (Appendix, Table A3). Second, we calculated the percentage of the total simulations where predicted displacements were not statistically different from the observed displacements (i.e. $P > 0.1$ in a gamma generalized linear model, GLM).

Ethical Note

This research project was approved by the Bioethics Committee at the Universidad Andrés Bello, Chile (No. 13/2015), by the Zoological Society of London's Ethics Committee (WLE709) and by permits No. 5666/2013, No. 230/2015 and No. 212/2016 of the Servicio Agrícola y Ganadero de Chile. Captured frogs were held in individual, disposable plastic bags filled with air and out of direct sunlight until they were processed. To reduce handling-related stress, all captured individuals were sampled only once within a primary capture occasion; for subsequent recaptures within these periods, individuals were identified without further sampling. Sampling did not take longer than 3 min per individual.

RESULTS

Captures

We made a total of 1028 captures of 311 different frogs (HUI1 = 192, HUI2 = 119). Of these, 144 (46.3%) were recaptured at least once across primary survey periods. We recorded a total of 328 daily displacements from 143 different individuals, 104 3-month displacements from 70 different individuals, and 116 annual displacements from 70 different individuals. The distribution of the number of displacements observed per frog at the three temporal scales is shown in the Appendix, Fig. A1. As expected due to the high temporal homogeneity of the environments used by the study populations, the annual displacement did not show strong temporal variation throughout the study duration (Fig. 1a; gamma GLM: $P = 0.99$) at the 3-month scale, there was some temporal variation in the observed displacements (Fig. 1a; gamma GLM: $P = 0.02$), which was related to a single time interval with relatively longer displacements (t3 in Fig. 1a; gamma GLM without this time

interval: $P = 0.30$). Overall, there was no clear evidence of temporal variation in the observed displacements and, therefore, observations from different time intervals were pooled for subsequent analyses.

Age-dependent Movement Behaviour: Empirical Data

Juveniles and adults displayed similar daily displacements (Fig. 1b; gamma GLMM: $P = 0.29$). Median daily displacement in juveniles and adults was 0.31 and 0.36 m, respectively. The largest daily displacement recorded among juveniles was 2.13 m, while in adults it was 14.56 m (Fig. 1b). At the 3-month scale, juveniles and adults also performed similar displacements (Fig. 1b; gamma GLMM: $P = 0.92$). The largest 3-month displacement registered (49.41 m; Fig. 1b) was performed by an adult male frog during the breeding season (during interval t4 in Fig. 1a). Median 3-month displacement was 3.60 and 4.40 m in juveniles and adults, respectively (Fig. 1b, Appendix, Table A2). In contrast, juveniles performed significantly longer annual displacements than adults (Fig. 1b; gamma GLMM: $P = 0.05$). In juveniles, median annual displacement was 15.29 m, while in adults it was 3.64 m (Fig. 1b, Appendix, Table A3).

Homogeneity of the Landscape

The polar direction (bearing angles) of the annual displacements were uniformly distributed both in HUI1 and HUI2 (Rayleigh test: both $P > 0.1$; Fig. 2). A similar pattern was found when the bearing angles were analysed separately during each time interval (Appendix, Fig. A2).

Age-dependent Movement Behaviour: Simulated Data

The Bayesian estimates of the parameters of the t distributions describing 3-month x - and y -direction movements, which were used to parameterize the MP model, are presented in the Appendix, Table A1.

Based on our two selection criteria, several MP model variations with a CRW for juveniles (with $r > 0.7$) and a SRW for adults, produced annual displacements similar to the empirical data (Fig. 3, Appendix, Table A3). From these, a model with $r = 1$ produced synthetic data that were not significantly different to the empirical data in 99.4% and 75.2% of the simulations (for juveniles and adults, respectively; Fig. 3). This model variation also led to similar gamma probability density functions (PDFs) of juvenile and adult annual displacement compared to those fitted to empirical data (Fig. 3c

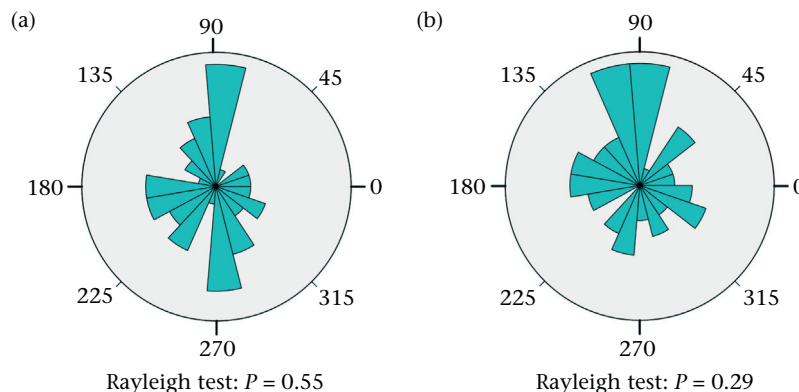


Figure 2. Rose graphs of the distribution of polar direction (bearing angle) of all recorded annual displacements of southern Darwin's frogs, *Rhinoderma darwinii*, captured at (a) HUI1 and (b) HUI2, Neltume, southern Chile.

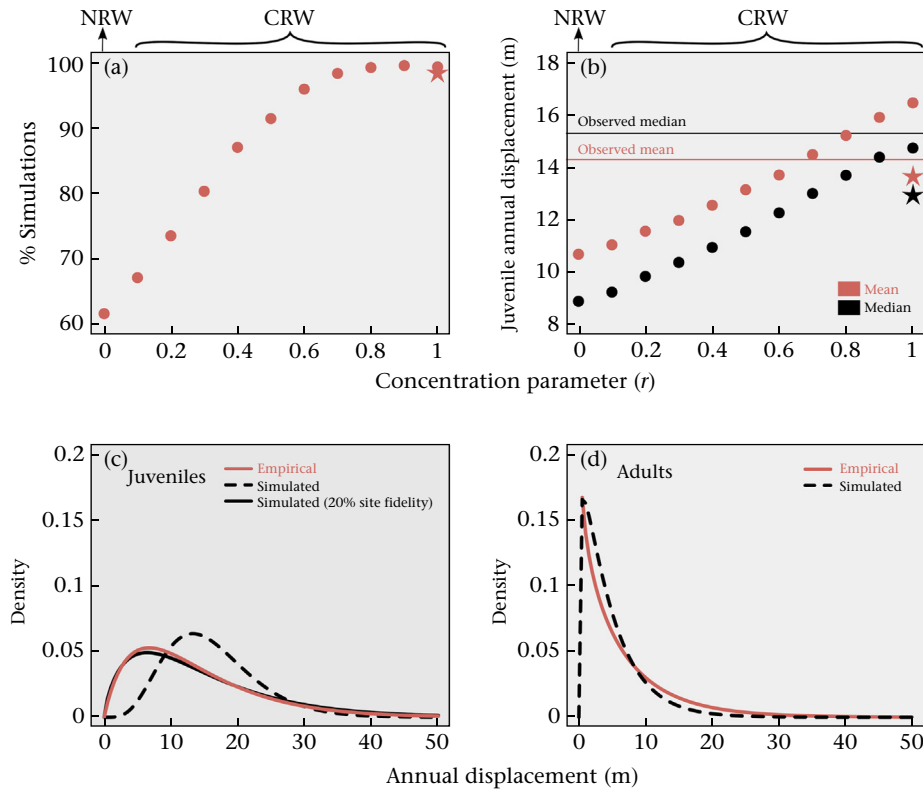


Figure 3. (a, b) Criteria used to test the performance of different variations of a model describing the annual displacement of southern Darwin's frogs, *Rhinoderma darwinii*, in a homogeneous landscape. In (a), for different concentration parameter (r) values of a wrapped Cauchy distribution, we show the percentage of 1000 simulations where synthetic and empirical juvenile annual displacement data were not significantly different (i.e. $P > 0.1$). NRW = noncorrelated random walk; CRW = correlated random walk. In (b) the mean and median annual displacement of juveniles is shown for different values of r . The stars in (a, b) represent a model variation where 80% of the juveniles move according to a CRW (with $r = 1$) and 20% move according to a SRW (i.e. they are site faithful). In (c, d) we show gamma probability density functions fitted to simulated (median from 1000 simulations; parameter values provided in the [Appendix, Table A4](#)) and empirical data. To produce simulated data, we used a model variation with a CRW for juveniles (with $r = 1$) and a SRW for adults. For the purposes of this model, frogs move in discrete 3-month time steps.

and d). In contrast, the MP model variations with a NRW or SRW for juveniles (i.e. no persistence in movement directionality and a stationary activity centre, respectively) showed a considerably poorer performance ([Fig. 3a and b, Appendix, Table A3](#)).

In juveniles, the gamma PDF fitted to simulated data had a slightly more negative skewness than the gamma PDF fitted to empirical data ([Fig. 3c](#)). If a percentage of juveniles are considered as site faithful (i.e. 20% of the juveniles moving according to a SRW), the resulting gamma PDFs are virtually identical to the fitted to empirical data ([Fig. 3c](#)), although the performance of this model variation was not equally enhanced based on the two selection criteria ([Fig. 3a and b](#)). Population heterogeneity in dispersal behaviour might be common in animals (e.g. [Denoël, Dalleur, Langrand, Besnard, & Cayuela, 2018](#)); this situation could account for a seemingly bimodal distribution of the annual displacements of juveniles ([Fig. 1b](#)).

DISCUSSION

Our results corroborate the existence of age-dependent dispersal in *R. darwinii*, with juveniles undergoing considerably longer annual displacements than adults ([Fig. 1b](#)), suggesting that natal dispersal is far more common than breeding dispersal in this forest amphibian. Our results also give support to the hypothesis that *R. darwinii* juveniles achieve dispersal by performing periods of routine movements integrated, over a longer (annual) temporal scale, along a nearly straight path.

Our empirical data suggest that *R. darwinii* frogs perform a slow natal dispersal lasting one year or more. Indeed, a visual inspection of the histogram of daily, 3-month and annual displacements revealed that, in the last case, juveniles (but not adults) performed a departure from what we considered a 'normal' movement behaviour for *R. darwinii* ([Fig. 1b](#)), which might be assumed as a signal for the occurrence of dispersal behaviour ([Nathan et al., 2012](#)). In other words, the natal dispersal of *R. darwinii* frogs seems not to be the result of fast, straight-line movements over a few days, as might be expected for species dispersing in heterogeneous landscapes ([Schtickzelle et al., 2007; Van Dyck & Baguette, 2005](#)). If this were the case, we would have expected to detect some of these fast, long-distance displacements at the daily or 3-month temporal scales. Dispersal duration in *R. darwinii* is likely influenced by the cost–benefit balance of different movement behaviours ([Bonte et al., 2012](#)). The evenly distributed polar direction of annual displacements ([Fig. 2](#)) reinforces the idea that *R. darwinii* individuals move across a highly homogeneous landscape. In these environments, in contrast to expectations in heterogeneous landscapes, the costs associated with a fast and straight-line dispersal movement behaviour (e.g. an increase in the risk of dying due to starvation or predation) might not be paid off by an overall reduction in dispersal costs ([Fahrig, 2007](#)), leading to the evolution of a relatively slow dispersal.

The slow natal dispersal of *R. darwinii* individuals is necessarily achieved through the recurrent use of routine movements used by individuals to search for food, shelter, and so on. At a high temporal resolution (e.g. daily movement steps), we expect, therefore, the

dispersal path of *R. darwinii* juveniles to be highly tortuous. The remarkably good performance of our MP model at predicting annual displacement based on 3-month movement steps, however, suggests that, at a coarser temporal resolution, the dispersal path of these frogs might look very straight. In other words, this suggests that even when dispersers perform routine movement behaviours over relatively short temporal scales, they maintain movement directionality over the year. For this species living in a highly homogenous landscape, this kind of dispersal behaviour likely reduces several of the costs associated with the transient stage of dispersal (Bonte et al., 2012). Specifically, the periods of routine movements might reduce risk costs, while the combination of these periods within a straight line maximizes dispersal distance while minimizing energetic costs (Brown et al., 2014; Fahrig, 2007).

The distribution of 3-month and annual displacements of *R. darwinii* adults were virtually identical (Fig. 1b), highlighting the existence of a stationary activity centre during adulthood in this species. Hence, the distribution of annual displacement in this age class was relatively well predicted by a simple stationary random walk (Fig. 3d). This evidence supports previous suggestions of high site fidelity in adults of this species (Crump, 2002; Valenzuela-Sánchez et al., 2014). The year-round movements of most *R. darwinii* adults likely represent routine movements associated with breeding and/or foraging activities within the adult home range rather than dispersal (Valenzuela-Sánchez et al., 2014), although a higher percentage of breeding dispersal, especially under conditions not present during our study (e.g. high population densities, food scarcity), might be expected as the result of condition-dependent dispersal (Bowler & Benton, 2005; Clobert et al., 2009; Matthysen, 2012).

Age-dependent dispersal is ubiquitous among some vertebrate groups, such as mammals and birds, where natal dispersal is far more common than breeding dispersal (Dale, Lunde, & Steifetten, 2005; Paradis, Baillie, Sutherland, & Gregory, 1998). In amphibians, our knowledge about age-dependent dispersal is limited. In pond-breeding amphibians, reviews suggest that natal dispersal is more common than breeding dispersal (e.g. Pittman, Osbourn, & Semlitsch, 2014; Semlitsch, 2008), but few empirical studies have verified this pattern (Berven & Grudzien, 1990; Schroeder, 1976; Sjögren-Gulve, 1998) while several others show similar rates of natal and breeding dispersal (Gamble, McGarigal, & Compton, 2007; Holenweg Peter, 2001; Reading, Loman, & Madsen, 1991; Smith & Green, 2006; Trenham, Koenig, & Shaffer, 2001). This could result from adults adjusting their dispersal decisions to the spatiotemporal variation of the breeding habitat (Cayuela et al., 2016; Trenham et al., 2001), which then affects breeding dispersal rates and distances in a context-dependent fashion. By contrast, in fully terrestrial amphibians, the relative environmental stability of the breeding habitat should result in low breeding dispersal rates because the ultimate drivers of dispersal are, most likely, the avoidance of kin competition and/or inbreeding depression (Bowler & Benton, 2005; Johst & Brandl, 1999; Perrin & Goudet, 2001; Szulkin & Sheldon, 2008). In these species, therefore, we expect juveniles to be the main dispersers, with natal dispersal being more pronounced than breeding dispersal. Our results for *R. darwinii*, along with those of a previous study of *Plethodon cinereus*, a fully terrestrial salamander from North America (Marsh, Thakur, Bulka, & Clarke, 2004), support this general prediction.

Conclusions

Our study provides rare empirical support for previous suggestions that dispersal in species inhabiting homogeneous landscapes are the result of routine movement behaviours (Fahrig, 2007). We additionally propose that, in these species, dispersal

can be the result of a combination of different movement behaviours, taking place at different temporal scales, within a single dispersal event. This opens new prospects in the study of dispersal behaviour, ecology and evolution, and highlights that the pervasiveness of nearly straight paths during dispersal could remain largely unappreciated (both theoretically and empirically), especially among species living in homogenous landscapes due to a bias imposed by the short temporal scales and high temporal resolutions at which this feature of movement behaviour has been traditionally studied.

Conflict of Interest

We declare that we have no conflicts of interest.

Data Accessibility

All data used in this manuscript are available at: <https://doi.org/10.5281/zenodo.1327549>. Codes are available upon request.

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Supplementary Data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.anbehav.2019.01.026>.

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Appendix

Spatial Cormack–Jolly–Seber Model: Structure and Parameters Estimation

We used the spatial Cormack–Jolly–Seber model (sCJS model; Schaub & Royle, 2014) to estimate the parameters of a *t* distribution describing 3-month displacements in Cartesian coordinates (i.e. *x*- and *y*-direction movements). This model was originally developed for the estimation of true survival probability using spatial capture–recapture data. However, in this study we only report results for the above-mentioned movement parameters. To homogenize the time intervals between primary survey periods, we

added dummy survey periods to our capture-history matrix (white boxes in Fig. 1a) and fixed the recapture probability at 0. During the duration of this study, survival probability of juveniles and adults was relatively constant over time at HUI1 and HUI2, and therefore, we constrained survival probability to be time-constant (Valenzuela-Sánchez et al., 2017). Survival probability was modelled as a function of age class (Valenzuela-Sánchez et al., 2017). Recapture probability was modelled as a function of plot and age class (Valenzuela-Sánchez et al., 2017). Movement parameters (scale and *df* of a *t* distribution) were constrained only by age class. We analysed the model in the program JAGS (Plummer, 2003) through the R package 'jagsUI' (Kellner, 2015). Vague priors

were used for all model parameters. We ran three chains of 500 000 Markov-chain Monte Carlo (MCMC) iterations with a burn-in of 20 000 without thinning. MCMC chains convergence was evaluated using the Gelman–Rubin \hat{R} statistic (i.e. \hat{R} values <1.1) and by a visual inspection of the chains.

Table A1

Bayesian estimates (mean [credible interval]) of the parameters of scaled *t* distributions of 3-month *x*- and *y*-direction movements of juvenile and adult southern Darwin's frogs, estimated using the spatial Cormack–Jolly–Seber model

	Scale	<i>df</i>
Juveniles	1.897 [1.038–3.144]	1.530 [1.034–2.633]
Adults	1.476 [1.189–1.854]	1.161 [1.010–1.419]

Table A2

Observed and simulated mean and median 3-month displacement of juvenile and adult southern Darwin's frogs

	Juveniles	Median	Adults	Median
	Mean		Mean	
Observed	6.01 (3.59–9.39)	3.60 (1.24–8.10)	6.67 (5.44–8.64)	4.40 (2.44–5.92)
NRW, <i>r</i> =0	10.73 (8.29–13.59)	9.12 (6.66–12.09)	14.65 (12.15–17.37)	12.76 (10.14–15.70)
CRW, <i>r</i> =0.1	10.96 (8.49–13.94)	9.34 (6.56–12.40)	15.03 (12.73–17.67)	13.15 (10.41–16.35)
CRW, <i>r</i> =0.2	11.14 (8.55–13.88)	9.56 (6.93–12.64)	15.26 (12.84–17.87)	13.50 (10.85–16.66)
CRW, <i>r</i> =0.3	11.42 (8.72–14.38)	9.87 (7.06–13.03)	15.75 (13.10–18.64)	14.00 (11.27–17.16)
CRW, <i>r</i> =0.4	11.84 (9.28–14.79)	10.29 (7.53–13.23)	16.17 (13.64–18.83)	14.49 (11.67–17.70)
CRW, <i>r</i> =0.5	12.31 (9.79–15.21)	10.86 (7.89–13.95)	16.75 (14.09–19.38)	15.10 (12.05–18.34)
CRW, <i>r</i> =0.6	12.90 (10.08–15.97)	11.50 (8.26–14.63)	17.52 (14.87–20.17)	15.95 (12.84–19.23)
CRW, <i>r</i> =0.7	13.73 (10.73–16.79)	12.43 (9.01–16.09)	18.73 (15.89–21.95)	17.33 (14.04–21.08)
CRW, <i>r</i> =0.8	15.34 (12.19–18.61)	14.19 (10.62–18.08)	20.58 (17.63–23.88)	19.23 (15.57–23.54)
CRW, <i>r</i> =0.9	18.33 (14.36–22.20)	17.29 (12.59–22.23)	24.02 (20.09–28.22)	22.88 (17.75–28.30)
CRW, <i>r</i> =1	42.60 (34.77–52.25)	42.39 (34.20–52.70)	53.00 (45.45–60.50)	53.00 (45.40–60.75)
SRW	0.57 (0.31–1.03)	0.28 (0.18–0.40)	0.84 (0.53–1.33)	0.40 (0.30–0.52)

NRW = noncorrelated nonstationary random walks; CRW = correlated nonstationary random walks; SRW = stationary random walks. Simulations are based on daily movement steps (model not presented in the main manuscript). The 2.5th–97.5th percentile range from 1000 simulations is shown in parentheses.

Table A3

Observed and simulated mean and median annual displacement of juvenile and adult southern Darwin's frogs

	Juveniles	Median	Adults	Median
	Mean		Mean	
Observed	14.30 (9.36–19.69)	15.29 (3.22–19.68)	6.48 (5.26–8.09)	3.64 (2.56–5.41)
NRW, <i>r</i> =0	10.71 (7.53–14.69)	8.92 (5.62–13.28)	25.17 (12.60–71.66)	10.00 (7.54–13.22)
CRW, <i>r</i> =0.1	11.07 (8.00–15.09)	9.27 (6.03–13.05)	25.84 (13.37–74.94)	10.51 (7.89–13.64)
CRW, <i>r</i> =0.2	11.59 (8.28–15.33)	9.87 (6.58–13.60)	25.67 (13.65–70.33)	11.12 (8.61–14.09)
CRW, <i>r</i> =0.3	12.00 (8.78–16.06)	10.40 (6.97–14.54)	26.08 (14.14–63.17)	11.62 (9.02–14.82)
CRW, <i>r</i> =0.4	12.58 (9.17–16.25)	10.97 (7.50–14.88)	27.40 (15.01–73.76)	12.38 (9.52–15.98)
CRW, <i>r</i> =0.5	13.17 (9.84–17.10)	11.57 (8.19–15.65)	28.05 (15.69–69.50)	13.10 (10.16–16.71)
CRW, <i>r</i> =0.6	13.73 (10.44–17.61)	12.29 (8.84–16.49)	28.74 (16.64–69.45)	13.91 (11.00–17.54)
CRW, <i>r</i> =0.7	14.51 (11.22–18.57)	13.03 (9.41–17.35)	28.85 (17.30–66.91)	14.62 (11.67–18.19)
CRW, <i>r</i> =0.8	15.24 (11.53–19.11)	13.72 (10.20–17.75)	30.99 (18.31–82.57)	15.51 (12.38–19.27)
CRW, <i>r</i> =0.9	15.93 (12.41–19.73)	14.41 (11.00–18.40)	33.20 (19.68–80.92)	16.53 (13.51–20.00)
CRW, <i>r</i> =1	16.48 (13.33–20.54)	14.76 (11.46–18.74)	33.58 (20.23–82.57)	17.37 (14.09–21.16)
CRW, <i>r</i> =1, 20% juveniles site faithful	13.74 (10.58–17.51)	12.95 (9.50–17.06)	n.e.	n.e.
SRW	4.16 (2.67–6.25)	3.06 (1.85–4.71)	4.86 (3.55–6.43)	2.87 (2.10–3.90)

NRW = noncorrelated nonstationary random walks; CRW = correlated nonstationary random walks; SRW = stationary random walks; n.e. = not evaluated. The mean (2.5th–97.5th percentile range) from 1000 simulations is shown.

Table A4

Gamma distribution parameters of observed and simulated annual displacement of juvenile and adult southern Darwin's frogs

	Juveniles	Rate	Adults	Rate
	Shape		Shape	
Observed	1.77 (0.99–4.22)	0.13 (0.06–0.35)	0.84 (0.66–1.06)	0.13 (0.10–0.18)
CRW, <i>r</i> =1	5.64 (3.03–13.15)	0.35 (0.17–0.89)	n.e.	n.e.
CRW, <i>r</i> =1, 20% site fidelity in juveniles	1.94 (1.19–3.90)	0.14 (0.08–0.29)	n.e.	n.e.
SRW	n.e.	n.e.	1.15 (0.85–1.69)	0.24 (0.14–0.47)

NRW = noncorrelated nonstationary random walks; CRW = correlated nonstationary random walks; SRW = stationary random walks; n.e. = not evaluated. Median (2.5th–97.5th percentile range) values from 1000 simulations are shown.

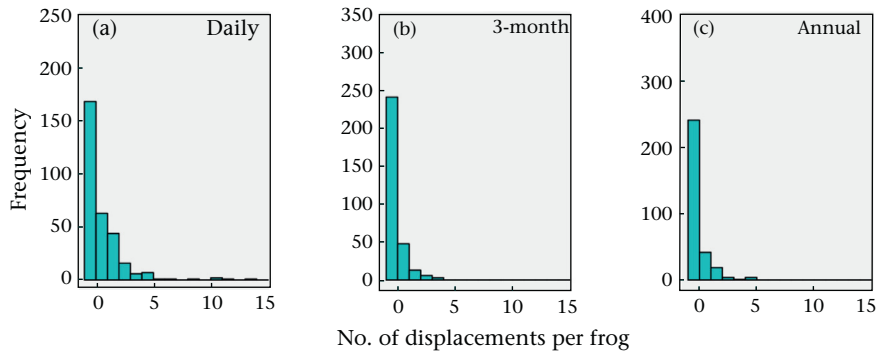


Figure A1. Distribution of the number of (a) daily, (b) 3-month and (c) annual displacements observed per frog at the three temporal scales investigated.

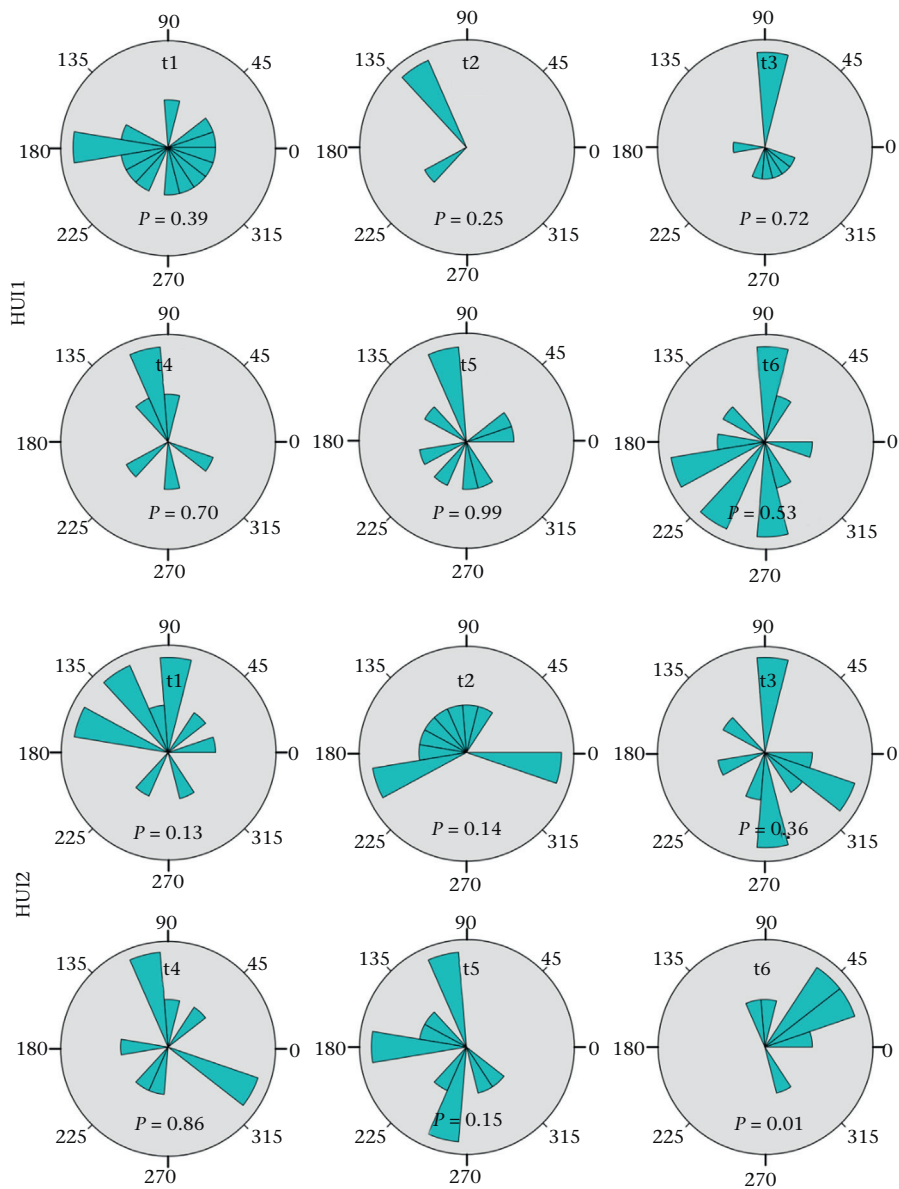


Figure A2. Rose graphs of the distribution of polar direction (bearing angle) of all recorded annual displacements of southern Darwin's frogs, *Rhinoderma darwinii*, at HUI1 and HUI2 during each primary capture occasion. *P* values from a Rayleigh's test of uniformity are shown.