Report

Current Biology

Differential Effects of Climate on Survival Rates Drive Hybrid Zone Movement

Highlights

- Climate and competition create survival differentials between hybridizing woodrats
- *Neotoma macrotis* has a consistent survival advantage in the contact region
- Survival advantages match the movement of the hybrid zone northward
- Hybrid zone shift could not be connected to climate without survival differentials

Authors

Elizabeth A. Hunter,
Marjorie D. Matocq, Peter J. Murphy,
Kevin T. Shoemaker

Correspondence

elizabethhunter@unr.edu

In Brief

Hunter et al. show that climate- and competition-driven survival differentials in two species of hybridizing *Neotoma* woodrats correspond to a northward movement of the hybrid zone. These results demonstrate the importance of delineating competing species' fitness differentials to predict how range limits will shift under a changing climate.

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Differential Effects of Climate on Survival Rates Drive Hybrid Zone Movement

Elizabeth A. Hunter,[1,2,*] Marjorie D. Matocq,[1] Peter J. Murphy,[1] and Kevin T. Shoemaker[1]
[1]Department of Natural Resources and Environmental Science; Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, Reno, NV 89557, USA
[2]Lead Contact
*Correspondence: elizabethhunter@unr.edu
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SUMMARY

Climate change has been implicated as driving shifts of hybridizing species' range limits [1, 2]. Whether and how much hybrid zones move depends on the relative fitness of hybridzing species under changing conditions [3, 4]. However, fitness is rarely linked to both climatic conditions and movement of hybrid zones, such that the relationship between climate change and hybrid zone dynamics remains tenuous [5]. Here we report how interactions between climate (seasonal precipitation) and competitor densities result in steep differentials in survival, which in turn drive hybrid zone movement for two woodrat species (*Neotoma fuscipes* and *N. macrotis*) in central California, USA. Using 6 years of capture-mark-recapture data, we found that the smaller-bodied species, *N. macrotis*, and hybrids had survival advantages over the larger-bodied *N. fuscipes* in the contact region during dry winters and wet springs. This pattern of differential survival, with *N. macrotis* having a consistent advantage over *N. fuscipes* during our study period, matched the spatial dynamics of the hybrid zone, which moved steadily north into *N. fuscipes* territory, with its estimated center moving ~150 m north in 6 years. Our findings provide a unique demonstration of range movements emerging from a complex interplay between climate and competition. Although all study site areas experienced the same climatic conditions, competitive effects created a complex spatial pattern of survival differentials, which in turn influenced hybrid zone movement. Characterization of fitness differentials derived from replicated demographic studies of contact regions between competitors should greatly improve our ability to understand and forecast climate-driven range dynamics.

RESULTS

We extensively trapped a narrow, linear, riparian woodland habitat where *Neotoma fuscipes* and *N. macrotis* come into contact in central California, capturing over 1,900 individuals and covering all known woodrat houses (nest, shelter, and food storage sites) within the study area and the genotypic gradients at either end of the contact region (Figure 1B). We used a spatial capture-recapture model to estimate effects of winter and spring precipitation, food availability (acorn production), and interspecific competition (relative heterospecific density) on survival rates of *N. fuscipes*, *N. macrotis*, and their hybrids (hereafter referred to as "types") over a 6-year period. We then investigated whether the direction of hybrid zone movement (or stability) matched patterns of relative survival among the types.

Greater winter precipitation had no effect on *N. fuscipes* survival ($\beta = -0.18$ to 0.18 [95% credible interval]), a negative effect on *N. macrotis* survival ($\beta = -0.33$ to 0.09), and a positive effect on hybrid survival ($\beta = -0.10$ to 0.44). Greater spring precipitation had negative effects on both *N. fuscipes* ($\beta = -0.53$ to -0.10) and *N. macrotis* survival ($\beta = -0.62$ to -0.18) and no effect on hybrid survival ($\beta = -0.32$ to 0.30). Differences between the species corresponded to respective differences in range-wide climate averages, with *N. macrotis* having a drier average range (Figure 1A) and experiencing greater negative effects of wet winters and springs on survival. However, even though *N. fuscipes* has a wetter range on average than *N. macrotis*, it still experienced a weak negative effect of wet springs on survival. In addition to precipitation effects, there was also a positive effect of previous-year oak (*Quercus* spp.) mast (acorn) production on survival for all types ($\beta = 0.01$ to 0.35).

How precipitation effects shaped survival differentials depended on the ecological context of competition. *N. macrotis* reached highest relative population densities in the south, *N. fuscipes* had highest densities in the north, and hybrids reached their highest relative densities in the contact region, although relative densities shifted over time, especially within the contact region (Figure 1B). Relative heterospecific density had no effect on *N. macrotis* survival ($\beta = -0.54$ to 0.41), whereas relative heterospecific density negatively affected survival rates of *N. fuscipes* ($\beta = -1.83$ to -0.50) and hybrids ($\beta = -3.68$ to -0.72). Thus, hybrid survival was highest in the contact region and *N. fuscipes* survival was highest in the northern, *N. fuscipes*-dominated region (Figure S1). Relative density for each type was not correlated with a proxy for habitat quality (density of houses within available riparian woodland habitat; $|r| < 0.5$ for all types), so these effects are unlikely to be a result of habitat differences.

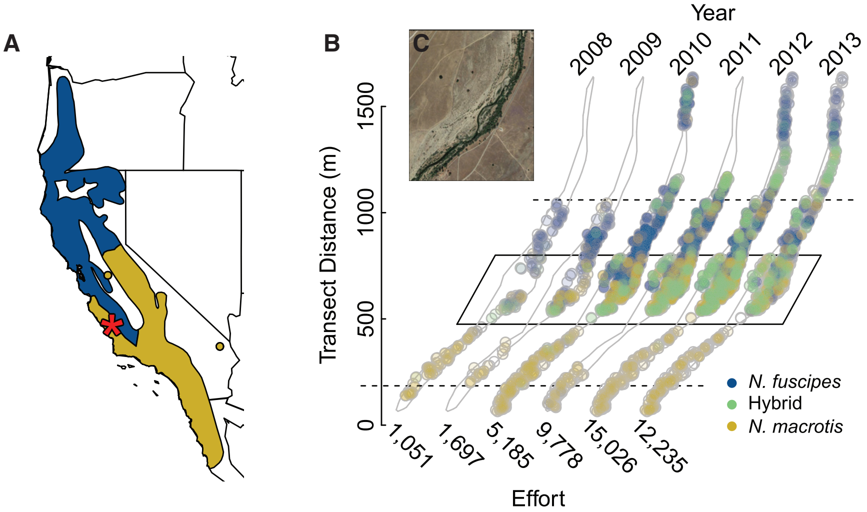

Figure 1. Distributions of *Neotoma fuscipes* and *N. macrotis*

(A) *N. fuscipes* (blue) and *N. macrotis* (yellow) ranges in western North America and the study area in the Salinas Valley (red asterisk).

(B) Survey effort and spatial distribution of types within the study area. Gray polygons correspond to the wooded riparian area in (C). Color opacity indicates the number of unique individuals caught in each trap in each period. Unfilled points are woodrat houses that were trapped but in which no individuals were caught. Numbers below the points indicate the "effort" or total number of trap nights in each year. The black polygon delineates the "contact region" (static position used in survival analyses), and the area between the dashed horizontal lines indicates where we looked for hybrid zone movement.

(C) An aerial photograph of the study site.

The combined effects of precipitation and interspecific competition resulted in large differences in survival rates among the types in the contact region, with *N. fuscipes* having a lower survival rate than *N. macrotis* in 4 of 6 years and a lower survival rate than hybrids in 2 of 6 years (Figure 2B). Survival differentials occurred under multiple combinations of winter and spring precipitation totals. Years with dry winters (2009, 2012, and 2013) were especially beneficial for *N. macrotis* (Figure 2C). In 2011, a year with a wet winter and spring, both species had lower survival rates, but hybrids had a relative survival advantage (hybrids had a survival advantage over *N. fuscipes* in years with wet springs; Figure 2F).

South of the contact region, *N. macrotis* always had higher survival rates than *N. fuscipes* (Figure S1). This was due to the almost complete dominance of *N. macrotis* in this area (Figure 1B) and the negative effects of interspecific competition on survival for *N. fuscipes*. In the north, none of the types had survival advantages throughout the entire study period (Figure S1). Thus, even though all areas of the study site experienced the same climatic conditions (inferred from the very small and topographically homogeneous study site), the ecological context resulted in a complex spatial pattern of survival differentials.

The pattern of differential survival rates in the contact region (Figure 1B), with *N. macrotis* having a consistent survival advantage over *N. fuscipes*, matched the spatial dynamics of the hybrid zone (Figure 3). There was a steady northward movement of the estimated hybrid zone center (i.e., the inflection point between pure *N. macrotis* and *N. fuscipes*) over time ($p = 0.001$, $R^2 = 0.93$), and it moved ~150 m north in 6 years (Figure 3A). One of the large northward jumps of the hybrid zone in 2013 corresponded to both *N. macrotis* and hybrids having greater survival than *N. fuscipes* in 2012. Similarly, another large jump northward in 2011 corresponded to higher survival rates for *N. macrotis* and marginally higher survival rates for hybrids in 2010. The only year with a slight southward movement of the hybrid zone, between 2011 and 2012 (Figure 3A), corresponded to low survival rates in both *N. macrotis* and *N. fuscipes* in 2011, the wettest year of the study period (Figure 2A).

DISCUSSION

The agreement between survival differentials among *Neotoma* types, driven by climatic and biotic factors (Figure 2), and the northward movement of the hybrid zone (Figure 3) provides compelling evidence for a critical link between climate and hybrid zone movement that would have been impossible to detect without understanding demographic factors. Survival differentials arose in the contact region due to the complex effects of climate (seasonal precipitation) and competitive interactions (Figure 2), which have both been shown to be influential in the dynamics of other hybrid zones, but rarely in combination [5, 6].

Interactions between climate and competition are likely to influence how boundaries between competing species shift under changing climates [7, 8], but delineation of the fitness mechanism is critical to making a direct link between climate change and boundary movements. For example, in a chickadee hybrid zone in North America, increasing temperatures are hypothesized to increase fitness of the southern species, *Poecile carolinensis*, relative to the northern species, *P. atricapillus*, shifting both species' range boundaries northward [1]. Similarly, warmer winters are hypothesized to increase overwintering probability for a southern species of cricket, *Allonemobius socius*, favoring its expansion compared to a northern species with which it hybridizes, *A. fasciatus* [2]. Yet, mate choice favoring southern males at range limits could also lead to a northward shift of the hybrid zone in both chickadees [9] and crickets [10] without any influence of climate change. Although climate is clearly a driver of hybrid zone movement for both cases, without a better understanding of the connection between climate and fitness, it is not clear how these hybrid zones will continue to move as the climate changes.

Interspecific competition may be more important than the degree of climate change for determining how species' distributions shift at the "trailing edges" of their ranges (lower latitude, warmer limit), and vice versa for "leading edges" (upper latitude, cooler limit) [11, 12]. The range edges of *N. fuscipes* and *N. macrotis* are complex, but at least within our study site, *N. macrotis* has a leading edge: as more *N. macrotis* settle in what was formerly *N. fuscipes* territory, both species' range

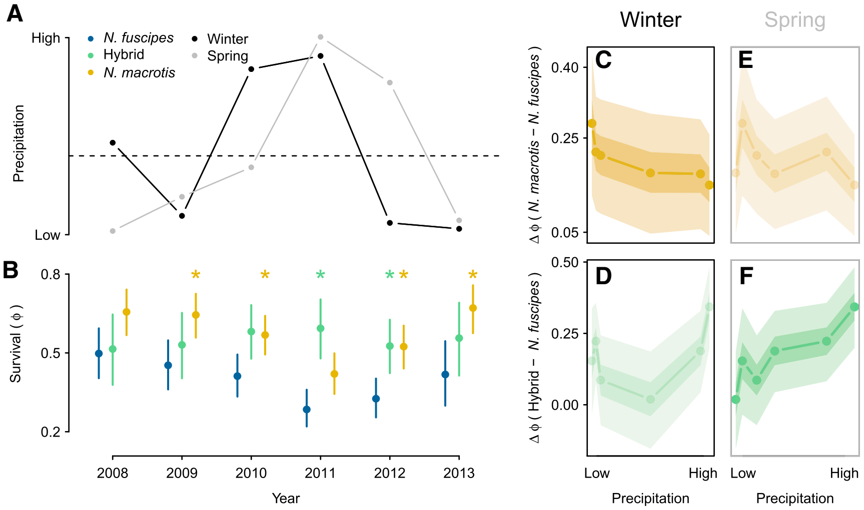

Figure 2. Effects of Precipitation on Survival in the Contact Region of *N. fuscipes* and *N. macrotis*

(A) Winter (black points) and spring (gray points) precipitation, shown as deviations from the 2008–2013 mean for each season (horizontal dashed line).

(B) Survival rates (only adult females are shown for clarity) for each type under each year's precipitation regime and observed relative heterospecific density for the contact region (means and 95% CIs). Asterisks (*) indicate years in which estimated survival of *N. macrotis* (yellow) and hybrids (green) had higher survival rates (non-overlapping 95% CIs) than *N. fuscipes* (blue) in the contact region. *N. fuscipes* did not have higher survival rates than the other two types in the contact region in any of the study years, nor did *N. macrotis* have higher survival than hybrids (or vice versa).

(C–F) Survival rate differentials between *N. macrotis* and *N. fuscipes* (C and E) and hybrids and *N. fuscipes* (D and F) as a function of winter (C and D) and spring (E and F) precipitation (points indicate mean differences, inner polygons indicate 50% CIs, and outer polygons indicate 95% CIs). Darker shaded plots (C and F) are those type-season combinations with more consistent trends that contributed to survival advantages over *N. fuscipes* in the contact region: drier winters for *N. macrotis* and wetter springs for hybrids. Note the different y axis scales.

See also Figures S1 and S2 and Table S1.

limits move north. Our results suggest that this movement is because climatic conditions were more favorable (drier) for *N. macrotis* in the study period. Conversely, *N. fuscipes* had a trailing edge to its distribution, not necessarily because climatic conditions were suboptimal, but due to competition with both *N. macrotis* and hybrids. For example, *N. macrotis* had a greater survival advantage over *N. fuscipes* during dry winters (Figure 2C), but this was entirely because of the effect of precipitation on *N. macrotis* survival, not on *N. fuscipes* survival (winter precipitation had no effect on *N. fuscipes* survival; Table S1). *N. fuscipes* could very likely survive in the climatic conditions of the *N. macrotis* range but would simply be outcompeted by *N. macrotis*. This pattern is seen in other hybridizing species, where the realized distribution of one species is constrained by competition (and hybridization) with the other species [13, 14].

In agreement with this pattern of *N. fuscipes* being at a competitive disadvantage, *N. fuscipes* (and hybrids) had lower survival rates in areas of higher heterospecific density (Table S1). This suggests that they are negatively affected by interspecific competition, although we cannot rule out an Allee effect (positive intra-specific density dependence), but no evidence supports this hypothesis for territorial woodrat species [15]. The results also imply that *N. macrotis* survival is not adversely affected by a greater relative density of *N. fuscipes*, which is surprising given that *N. fuscipes* is the larger and more aggressive species [16]. However, aggressive interactions between individuals are more likely to be directed at improving mating chances than at increasing survival and may actually decrease survival rates [17, 18]. Competitive interactions may also be related to resource acquisition abilities. Although larger animals are generally competitively dominant when resources are abundant, smaller competitors can prevail when resources are scarce [19, 20]. These woodrat species forage on consistently available oak leaves, but it is possible that acorns are a less available and competitively sought-after resource (we found a positive effect of acorn production on survival, suggesting that acorns are an important food resource [21]). Although acorn abundance was not correlated with precipitation within our study period, long-term drought can decrease acorn production [22]. California (and the study site) was in a drought during the majority of the study period (Figure S2) [23], potentially indicating that our study occurred during a time of scarcity that affected competitive dynamics.

Resource availability in arid and semi-arid ecosystems is typically governed by precipitation, but the outcomes of precipitation events on population abundance, competition, and range dynamics are often complex and non-linear [24, 25]. Because of the complexities associated with precipitation, many studies of climate change effects on hybrid zone and range edge dynamics have focused on temperature shifts, which tend to be more consistently directional [1, 26, 27]. But precipitation regimes will also be altered by climate change, often complicating directional effects of warming temperatures [28, 29]. Given the potential importance of precipitation to differential fitness within hybrid zones and the resulting range edge dynamics [3, 30], it will be important to gain a deeper understanding of the mechanistic pathways and intermediate effects that connect precipitation effects (such as those presented here) to fitness to make more accurate predictions under climate change.

Counter to our findings, we hypothesized that all types would survive at higher rates during wet periods. Positive effects of precipitation on rodent abundance have been found in other arid and semi-arid ecosystems [31, 32], with a proposed mechanism of precipitation causing ephemeral plant growth leading to increased rodent reproduction and abundance [24, 31]. However, woodrats primarily eat low-quality, consistently available forage (e.g., oak leaves [33]), so the precipitation effects that we detected may be unrelated to food availability. A possible

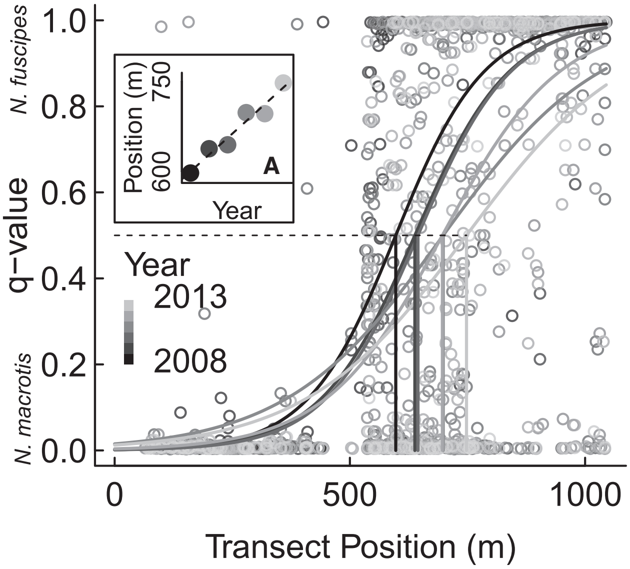

Figure 3. Spatial Position of the Hybrid Zone

Each point represents an individual on the first capture in each year (gray scale). The center of the hybrid zone for each year is estimated as the inflection point on a logit curve between pure types (0, *N. macrotis*; 1, *N. fuscipes*). Vertical lines show the transect position at the estimated center (q = 0.5, dashed horizontal line).

(A) Center points as a function of time.

explanation for negative precipitation effects on survival is that wetter periods dampen woodrat houses, causing damage (requiring energy and exposure to predators to repair or replace [21, 34]) and potentially spoiling food stores of acorns [21]. A wet house could also favor woodrat parasites such as nest mites, fleas, and ticks [35, 36] that might negatively affect survival. In addition, wetter periods are sometimes associated with disease outbreaks in other semi-arid rodent species [37]. Differences among the types in the effect of precipitation on survival provide a way to test these hypotheses by looking for type differences in diet (or food storage), parasites, and disease.

Given the variability of precipitation in central California, the hybrid zone movement that we observed may have been temporary. In previous years and decades, the site experienced wetter conditions (Figure S2) that may not have provided the survival advantage to *N. macrotis* that is necessary for northward movement of the hybrid zone. In fact, the position of the contact region within the *N. macrotis* range (western Salinas Valley of California; Figure 1A) led to previous hypotheses that *N. fuscipes* was actually expanding into *N. macrotis* territory [38]. However, mtDNA introgression patterns did not support this hypothesis [38], and our current results suggest that at the very least *N. macrotis* has had a consistent 6-year movement into *N. fuscipes* territory (though small, the 150 m movement of the hybrid zone is much greater than typical lifetime movement distances of less than 100 m [39], indicating that movement is not caused by dispersal). Currently, the lack of a survival differential north of the contact region (Figure S1) may act as a barrier to continued movement, but only if relative densities remain at their present levels. Future climatic conditions may tip the survival advantage to one type or the other, pushing relative densities over a competitive threshold that leads to more movement of the hybrid zone. Although the drought that started in late 2011 has ended as of spring 2017, drier conditions could continue with climate change [40], which would favor continued expansion of the *N. macrotis* range limit.

Prediction of future hybrid zone dynamics will be aided by a mechanistic understanding of the connections between fitness (in this case, survival), climate, and ecology of the hybridizing species. Determining the effects of climate on fecundity is also an important missing piece of the puzzle, as there may be complicating tradeoffs between survival and fecundity under different climatic and ecological conditions [41]. However, survival often is a better indicator of overall fitness than fecundity for iteroparous organisms [42]. Here, we have demonstrated the importance of linking fitness to hybrid zone dynamics to understand the effects of climate. Without knowledge of the interacting effects of seasonal precipitation and competition on survival, we would not be able to link the northward movement of the *Neotoma* hybrid zone to climate. Thus, making these linkages could reveal that even more hybrid zones are influenced by climate than previously thought [5, 6], emphasizing the need for additional empirical work as the climate continues to change.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - ○ Trapping Details
  - ○ Genetic Assignments
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - ○ Survival Model
  - ○ Movement of Hybrid Zone
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and one table and can be found with this article online at https://doi.org/10.1016/j.cub.2017.11.029.

AUTHOR CONTRIBUTIONS

M.D.M. conceived and designed the study and oversaw data collection. P.J.M. organized, databased, and quality checked the field data. E.A.H. and K.T.S. conducted the data analysis. E.A.H. wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
1,576 woodrat (*Neotoma* spp.) tissue samples	Authors	N/A
Deposited Data		
Data reported in this paper	Authors	https://doi.org/10.17632/chgz9bkxf8.2
Woodrat (*Neotoma* spp.) demographic data (including assigned types)	Authors	https://github.com/kevintshoemaker/woodrat-hybridzone
Software and Algorithms		
R: A language and environment for statistical computing.	[43]	https://www.r-project.org
JAGS: analysis of bayesian hierarchical models	[44]	http://mcmc-jags.sourceforge.net
Original analysis code	Authors	https://github.com/kevintshoemaker/woodrat-hybridzone

CONTACT FOR RESOURCE SHARING

Further information and requests may be directed to, and will be fulfilled by, the Lead Contact, Elizabeth A. Hunter (elizabethhunter@unr.edu).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The hybridizing population of *N. fuscipes* and *N. macrotis* was studied in the wild. All trapping and handling activities were conducted under a scientific collection permit from the California Department of Fish and Wildlife, protocols approved by the University of Nevada, Reno Institutional Animal Care and Use Committee, and in accordance with the guidelines of the American Society of Mammalogists [45]. We captured 1,914 individuals and collected tissue samples from 1,576 individuals (including males, females, adults, and juveniles).

METHOD DETAILS

Trapping Details

We collected field data along a 2-km stretch of the Nacimiento River, concentrating on the narrow contact area between *N. fuscipes* and *N. macrotis* [38]. The study area, on the Camp Roberts Military Reservation, lies 6.5 km northwest of San Miguel, CA at the southern end of the Salinas Valley (35.775136, −120.795083; Figure 1). The riparian habitat along the Nacimiento river is dominated by several species of oak (*Quercus* spp.), willow (*Salix* spp.), and elderberry (*Sambucus* spp.), and is highly restricted to the river edge, although the extent of habitat is wider in the center of the study site (where hybridization is most intense). We surveyed the area from 2008-2013, but capture effort varied over the years of the study, with substantially more effort (in both time and space) in 2010-2013 (Figure 1B). Captures occurred in May-June 2008, March-August 2009, April-August 2010, April-October 2011 and 2012, and April-Sep 2013, with most effort and captures in the April-August period. At first capture we sexed, aged, weighed, and individually ear-tagged each animal, and collected tissue via ear biopsy for genetic analysis.

We captured woodrats using Tomahawk live-traps that were open for three consecutive nights at a house, in rotating, overlapping traplines with ~20-200 houses trapped per week (trapping intensity was greater during times of juvenile emergence). We added new houses to traplines as they were discovered. Houses were trapped for an average of 38 nights over the course of the study, with 1,174 houses trapped and a total of 44,972 trap-nights. We captured 1,914 individuals in the study area with 13,619 captures (mean 7.1 captures/individual, range 1-71 captures/individual).

Genetic Assignments

All individuals sampled from 2008-2012 were genotyped at 15 microsatellite loci. We used STRUCTURE 2.3.4 [46, 47] to classify individuals as pure or hybrid using the procedures outlined in Coyner et al. [38]. We classified individuals as hybrids when they had *q*-values between 0.1-0.9 for either parental genome; individuals were classified as pure *N. macrotis* or pure *N. fuscipes* if they had $q > 0.90$ for either parental genome (we were able to identify F1 and backcrossed hybrid types, but due to smaller sample sizes and overall similar survival effects for each of these hybrid types, we lumped all hybrids together in a single group). We classified 720 individuals as *N. fuscipes*, 562 as *N. macrotis*, 257 as hybrids, and 37 were unable to be genotyped. Trapping in 2013 was conducted primarily to recapture previously caught individuals, thus newly caught individuals in 2013 were not genotyped (N = 338, these individuals did not factor into type-specific parameter estimates). Surveys in habitat ~2 km to the northeast and southwest of the study area in 2008 and 2010 confirmed that the study area was the hotspot of contact between the two species, with no *N. macrotis* detected in the north (60 *N. fuscipes* and 10 hybrid [all backcrosses to *N. fuscipes*] individuals captured), and no *N. fuscipes* detected in the south (75 *N. macrotis* and 2 hybrid [both backcrosses to *N. macrotis*] individuals captured).

QUANTIFICATION AND STATISTICAL ANALYSIS

Survival Model

We estimated survival rates (φ) using an open-population, spatially explicit, capture-recapture analysis, implemented in a Bayesian framework to obtain posterior distributions through Markov Chain Monte Carlo (MCMC) simulations in the computer program JAGS [44], which was called from the R environment via the R2JAGS package [43].

Spatially explicit capture-recapture

Given woodrats' strong site fidelity and the spatiality inherent in our field data collection process (woodrats are typically captured at houses within their home range), a spatially-explicit capture-recapture (SECR) model is appropriate. SECR models incorporate spatial information from captures in order to reduce uncertainty about capture probability, with the assumption that individuals are more likely to be caught in traps closer to (or within) their home range than those farther away from their home range [48]. We created a SECR model by assigning houses within the study area to 12 equally-spaced quadrants (six quadrants in the northern, *N. fuscipes*-dominated region, two in the contact region, and four in the southern, *N. macrotis*-dominated region, Figure S3). The study period comprised 11 primary capture periods, with an early (March – June 30) and late (July 1 – October) summer period for each year (except 2008, which only has an early summer period). The July 1 threshold between early and late summer was chosen based on the timing of birthing pulses in May and July.

The observed captures of each individual in each quadrant and time period are binomially distributed, so that for the i^{th} individual, t^{th} period, and k^{th} quadrant:

$$y_{itk} \sim Bin(\lambda_{itk}, \tau_{tk}) \quad \text{(Equation 1)}$$

where y_{itk} is the observed number of captures of individual i in period t in quadrant k, λ_{itk} is the capture probability and τ_{tk} is the effort (total number of trapnights). Capture probability is a function of the squared distance between a given quadrant, q_k, and the quadrant occupied by the individual i during period t, q_{it} (quadrant distance is the average distance of all houses in a quadrant to all houses in quadrant k):

$$\lambda_{itk} = \lambda_0 \exp\left(\frac{(q_{it} - q_k)^2}{2\sigma^2}\right) z_{it} \quad \text{(Equation 2)}$$

where λ_0 is the baseline probability of detection within an individual's current quadrant, z_{it} is the latent alive/dead state of an individual ($z_{it} = 1$ indicates alive and $z_{it} = 0$ indicates dead), and σ is a parameter of the half-normal distribution that approximates the average home range size radius (we estimated a separate σ for females and males). Individuals have a probability of moving from their current quadrant (any house within the quadrant) to other quadrants as a function of the time period duration (fraction of a year between median dates of each trapping period).

Open-population survival model

We used a Cormack-Jolly-Seber formulation to model survival between periods. Survival rates were modeled as a logit-linear function of intrinsic traits and environmental covariates:

$$logit\left\{(\varphi_{it})^{\frac{1}{per}}\right\} = \beta_0 + \beta_1 \cdot cov_{it} + \ldots + \beta_{18} \cdot cov_{it} \quad \text{(Equation 3)}$$

Where φ_{it} represents survival rate between trapping periods, *per* represents the interval between sampling periods in units of years, β_0 represents the baseline mean annual survival rate on the logit scale, β_1 - β_{18} represent logit-linear effects of various covariates, cov_{it}, on survival (Table S1). Although the survival (φ_{it}) term technically represents apparent survival (compound parameter indicating death or permanent emigration), we interpret this term as true survival because suitable habitat is restricted to the riparian area immediately adjacent to the river (only wooded area), thus emigration from this habitat is most likely functionally equivalent to mortality.

Intrinsic covariates included type (*N. fuscipes*, *N. macrotis*, hybrid), age, and sex. Not all captured individuals were genotyped – for these unknowns, we used the observed relative proportion of each type in each period and quadrant to probabilistically assign types using multiple imputation [49]. Assignments were not fixed, but instead an individual could be assigned a different type for each MCMC iteration (based on the probability of being each type drawn from known distribution information in each quadrant and period). We used two age classes (juveniles and adults), where juveniles remained juveniles for the entire year in which they were first caught (maximum time in juvenile state would be spring to early fall of the same year). Some juveniles were difficult to sex and a small number of adults that escaped the handler prior to sexing were classified as sex unknown; we used the overall sex ratio to assign prior probability of being male or female for these few unknown individuals.

Extrinsic covariates included relative density of heterospecifics (to estimate effects of interspecific competition), an index of acorn productivity or ''mast,'' and precipitation. We used the observed relative proportion of each type in each period and quadrant as an indicator of the relative density of heterospecifics. To ensure that estimated effects of relative heterospecific density were not simply artifacts of habitat quality differences within the study site, we estimated habitat quality as the density of houses within available riparian woodland habitat. We digitized woodland habitat using a Google Earth aerial image of the site from 2013 (and verified that tree cover was consistent throughout the study period using images from 2010 and 2007). We then calculated the density of houses within the habitat surveyed in each study period as a measure of habitat quality (because houses occupied all available habitat, higher density of houses indicates higher quality habitat). Relative heterospecific densities were not correlated ($|r| < 0.5$) with habitat quality for any of the types.

Mast productivity was estimated using data from the California Acorn Survey's Pozo site (~65 km from field site, in similar orographic position [22]). We used prior year averaged acorn counts from three common oak species (*Quercus agrifolia*, *Q. douglasii*, and *Q. lobata*) to create a mast index. Precipitation data were from the Paso Robles Municipal Airport NOAA weather station (~20 km from field site, in similar elevation and orographic position), and we summed precipitation totals within winter (October-February) and spring (March-May) to create two precipitation covariates. Prior to analysis, we standardized environmental covariates (mast index and precipitation) using z-score scaling to improve model convergence.

Model Fitting

We investigated separate effects of the extrinsic covariates on survival of each type, but where there was not substantial support for doing so (no differences in effects among types) or adding the effect meant the model could not converge, a single effect was estimated. We assigned uninformative uniform prior probability distributions to all free parameters (Table S1). We ran three independent Markov chains, discarding the first 10,000 MCMC samples as a burn-in and storing every fifth sample of the remaining 20,000 MCMC iterations for further analysis. We tested for Markov chain convergence to a stationary posterior distribution with the Gelman-Rubin diagnostic [50]. We summarized posterior distributions for all parameters with the mean of all MCMC samples as a point estimate and the 2.5 and 97.5 percentiles of the MCMC samples as a 95% credible interval [50].

Goodness-of-fit

To assess goodness-of-fit of our final model, we used a ''Bayesian p value,'' a measure of the discrepancy between the actual dataset and data simulated under the estimated parameters [51]. Bayesian p values close to 0.5 (and far from 0 or 1) indicate a well-fitting model. We simulated 10,000 new datasets by drawing parameter values from posterior distributions (MCMC samples) with replacement and calculating survival and capture rates while conditioning on the exact same trapping effort and numbers of new individuals of each sex, age, and type in each period as in the observed data. We then counted the number of individuals known to be alive in each period (captured at least once) and the proportion of those individuals that were seen during any later period. We used the discrepancy in these proportions between actual and simulated datasets to calculate the Bayesian p value [52]. The Bayesian p value of 0.36 indicated adequate fit to the data.

Movement of Hybrid Zone

We tested for movement of the hybrid zone by fitting logistic regressions to *q*-values as a function of transect distance (UTM Northing in meters) for each survey year (due to biases in spatial survey effort among years, the spatial extent for this analysis was the minimum and maximum transect distance trapped among all years [Figure 1B]). Based on these logistic regression curves, we calculated the transect position at which the inflection point occurred (q-value = 0.5) to estimate the approximate center of the hybrid zone [1, 53], and determined whether the hybrid zone center was moving over time using a linear regression. To determine whether unequal sampling among years (Figure 1B) influenced the outcome of this analysis, we re-ran the analysis 100 times, sampling such that each year had the same number of data points. This analysis still produced significant results (only one run out of 100 had a p value > 0.05), and the average hybrid zone movement was the same as with all data points, so we present the original analysis.

DATA AND SOFTWARE AVAILABILITY

The accession number for the data reported in this paper is Mendeley Data: https://doi.org/10.17632/chgz9bkxf8.2. Scripts for running all analyses (in programs R and JAGS) are posted on GitHub: https://github.com/kevintshoemaker/woodrat-hybridzone.