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Biol. Lett. 2007 **3**, 646-650
doi: 10.1098/rsbl.2007.0368

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Two waves of diversification in mammals and reptiles of Baja California revealed by hierarchical Bayesian analysis

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Many species inhabiting the Peninsular Desert of Baja California demonstrate a phylogeographic break at the mid-peninsula, and previous researchers have attributed this shared pattern to a single vicariant event, a mid-peninsular seaway. However, previous studies have not explicitly considered the inherent stochasticity associated with the gene-tree coalescence for species preceding the time of the putative mid-peninsular divergence. We use a Bayesian analysis of a hierarchical model to test for simultaneous vicariance across co-distributed sister lineages sharing a genealogical break at the mid-peninsula. This Bayesian method is advantageous over traditional phylogenetic interpretations of biogeography because it considers the genetic variance associated with the coalescent and mutational processes, as well as the among-lineage demographic differences that affect gene-tree coalescent patterns. Mitochondrial DNA data from six small mammals and six squamate reptiles do not support the perception of a shared vicariant history among lineages exhibiting a north-south divergence at the mid-peninsula, and instead support two events differentially structuring genetic diversity in this region.

Keywords: approximate Bayesian computation; comparative biogeography; statistical phylogeography

1. INTRODUCTION

Comparative phylogeography is a powerful approach for elucidating the historical processes responsible for shaping genetic diversity across co-distributed species (Avise 2000; Arbogast & Kenagy 2001). Baja California, a peninsula 1300 km long with a complex tectonic history, is inhabited by many co-distributed species that share the common phylogeographic pattern of genetic divergence across the middle of the peninsula (Riddle *et al.* 2000a). A seaway spanning the

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2007.0368> or via <http://www.journals.royalsoc.ac.uk>.

mid-peninsula is most often invoked as the vicariant event responsible for producing this shared genealogical pattern (Lindell *et al.* 2006), but this hypothesis is controversial owing to a lack of any geological evidence (Crews & Hedin 2006). Despite the effort expended on debating the existence of a putative seaway, previous studies did not consider that the appreciable differences in genetic divergence observed across different lineage pairs separated at the mid-peninsula are an indication that diversification may have occurred in multiple waves. Thus, whether the shared genealogical divisions at the mid-peninsula occurred simultaneously or non-synchronously due to multiple events remains untested.

Inferring the number of events responsible for structuring genetic diversity is imperative for understanding evolutionary processes, especially when the outcome of such analyses fuels conclusions concerning historical biogeography. Multiple temporally and spatially distinct historical events can produce similar phylogeographic patterns among co-distributed taxa and thus appear as a single event (Riddle & Hafner 2006). These alternatives are indistinguishable without an explicit examination of the timing of population divergence. The objective of this study is to statistically test the simultaneous vicariance hypothesis for the small mammals and squamate reptiles sharing concordant mitochondrial DNA (mtDNA) divergence at the mid-peninsula of Baja California.

We use a hierarchical Bayesian model to test multi-taxa hypotheses while explicitly accounting for uncertainty in taxon-specific demographic parameters that will differentially affect gene-tree coalescence. Instead of calculating the likelihood function in this cumbersome parameter-rich hierarchical model, we use approximate Bayesian computation (ABC) to replace the data with a summary statistic vector (Beaumont *et al.* 2002). The core advantage gained by this replacement is the ability to evaluate more complex models, such as those that apply to multi-species datasets (Hickerson *et al.* 2006a).

2. MATERIAL AND METHODS

(a) Samples

We analysed 12 mtDNA datasets, representing six small mammals and six squamate reptiles that share concordant phylogeographic breaks at the mid-peninsula. Properties of the sampling intensity and nucleotide composition of these datasets and their sources are listed in table 1.

(b) Hierarchical Bayesian model of multi-species divergence

The hierarchical Bayesian model tests for simultaneous vicariance under the ABC framework, which is implemented in the MSBAYES software pipeline (Hickerson *et al.* 2007). For full details of the model, see Hickerson *et al.* (2006b) and the electronic supplementary material. We use the hierarchical ABC model to estimate the hyper-parameters that quantify variability in the Y divergence times. This includes the number of possible divergence times per Y taxon-pairs (Ψ), the mean divergence time across the Y taxon-pairs ($E(\tau)$) and the ratio of the variance of τ to the mean of τ ($Q = \text{var}(\tau)/E(\tau)$). Although Ψ is a discrete hyper-parameter, it is estimated as a continuous hyper-posterior due to our implementation of ABC employing the local regression method of Beaumont *et al.* (2002). Each set of hyper-posteriors was constructed from 1000 accepted draws from $K=500\,000$ simulated draws from the hyper-prior using the acceptance/rejection with local regression algorithm (Beaumont *et al.* 2002). We express divergence times in units of millions of years by assuming a generation time of 2 years and use a range of calibration rates (1, 2.0 and 3.0% Myr⁻¹) that reflect our uncertainty in the actual rate of molecular evolution.

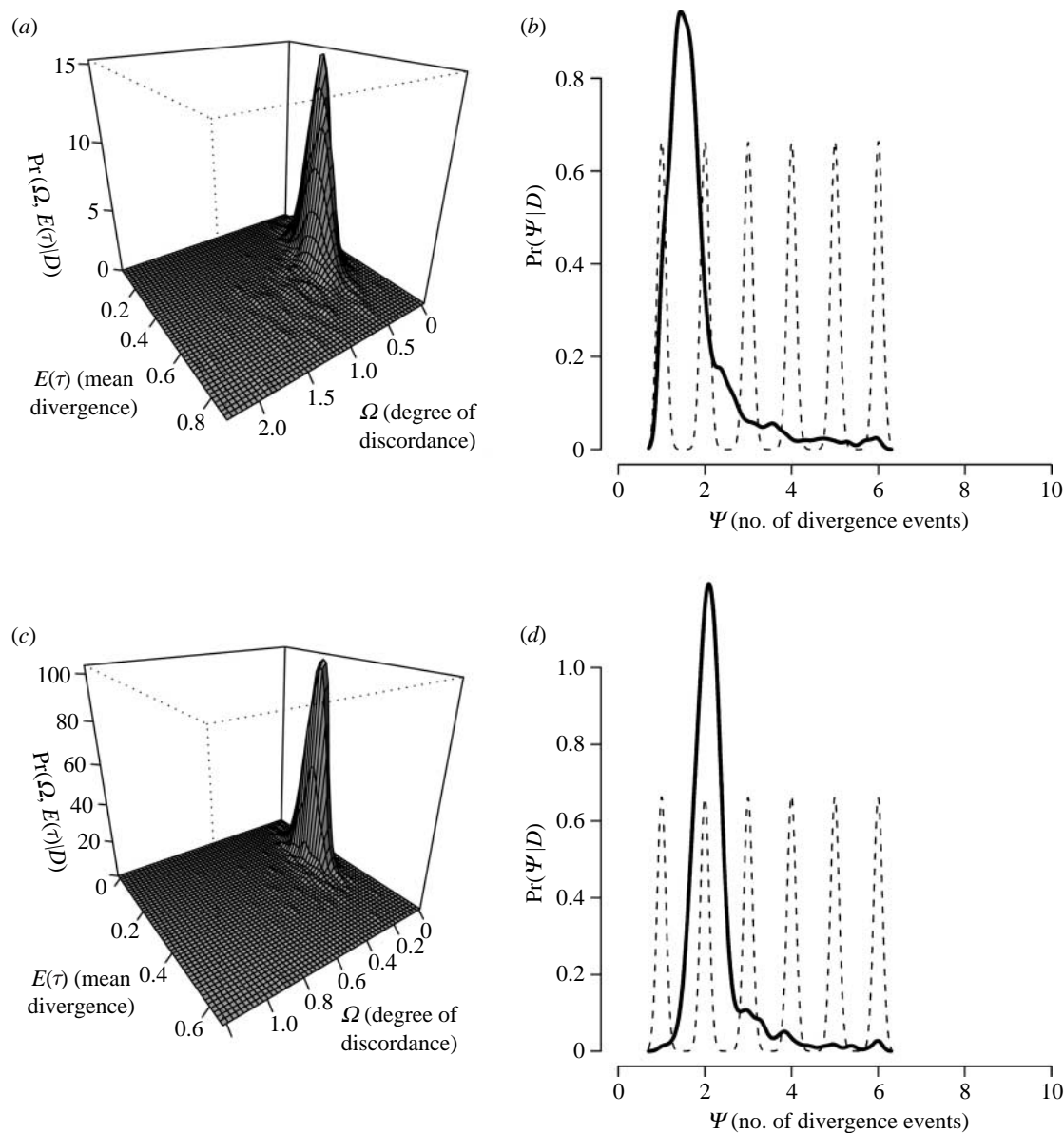


Figure 1. Posterior estimates of temporal concordance among six lineage pairs of (a,b) mammals and (c,d) reptiles spanning the mid-peninsula of Baja California. (a,c) Joint posterior probability densities for $E(\tau)$. (b,d) Posterior probability densities for Ψ , the number of divergence times per six lineage pairs. (a) $\Omega=0.30$, Bayes factor=0.07; (b) $\Psi=1.39$; (c) $\Omega=0.15$, Bayes factor=0.25; (d) $\Psi=2.11$.

Table 1. Mammals and reptiles with phylogeographic breaks at the mid-peninsula of Baja California used to test the simultaneous vicariance hypothesis. (Transition/transversion estimates were calculated in PAUP v. 4.0b10 under the HKY model of nucleotide substitution.)

	mtDNA gene	length (bp)	sample size (north/south)	percentage of mtDNA divergence	source	
mammals						
	<i>Ammospermophilus leucurus</i>	<i>Cytb</i>	548	52/25	4.7	Whorley <i>et al.</i> (2004)
	<i>Chaetodipus arenarius</i>	<i>COIII</i>	699	22/12	10.1	Riddle <i>et al.</i> (2000a)
	<i>Chaetodipus baileyi</i>	<i>COIII</i>	699	34/5	2.1	Riddle <i>et al.</i> (2000c)
	<i>Dipodomys merriami</i>	<i>COIII</i>	699	6/6	1.1	Riddle <i>et al.</i> (2000a)
	<i>Peromyscus eremicus</i>	<i>COIII</i>	699	10/8	3.4	Riddle <i>et al.</i> (2000b)
	<i>Thomomys bottae</i>	<i>Cytb</i>	500	13/123	2.0	Trujano-Alvarez (2007)
squamates						
	<i>Callisaurus draconoides</i>	<i>Cytb, ATPase 6</i>	1953	14/23	4.8	Lindell <i>et al.</i> (2005)
	<i>Phrynosoma coronatum</i>	<i>ND1, ND2</i>	2002	22/10	4.0	Leaché <i>et al.</i> (submitted)
	<i>Uta stansburiana</i>	<i>ATPase 6</i>	890	8/7	3.9	Upton & Murphy (1997)
	<i>Sceloporus zosteromus</i>	<i>ND4</i>	825	8/4	7.0	Leaché & Mulcahy (in press)
	<i>Pituophis catenifer</i>	<i>ND4</i>	893	9/4	5.1	Rodriguez-Robles & Jesús-Escobar (2000)
	<i>Trimorphodon biscutatus</i>	<i>ND4</i>	817	15/3	1.6	Devitt (2006)

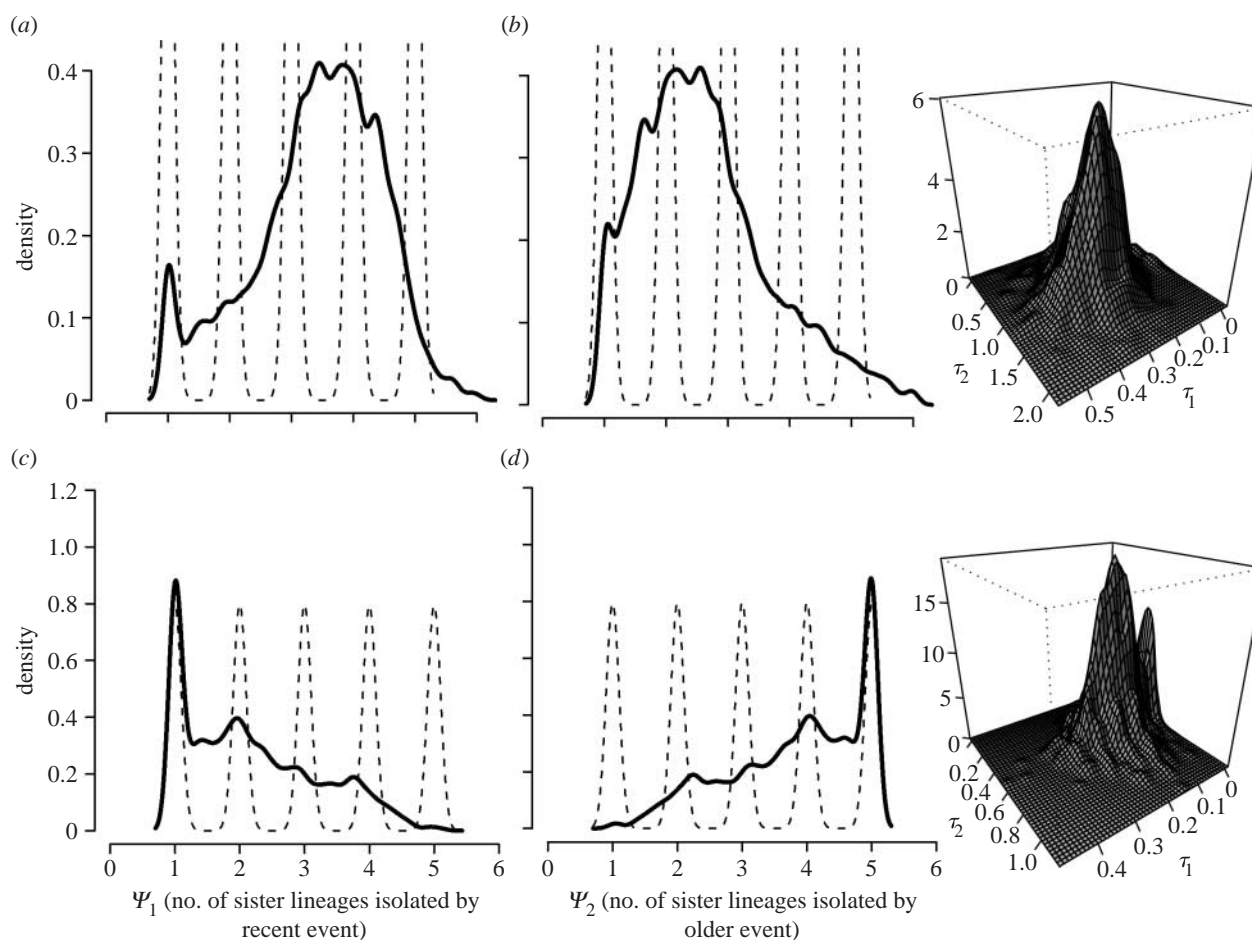


Figure 2. Posterior densities of Ψ_1 , Ψ_2 , τ_1 and τ_2 for the mammals and reptiles under the model constrained for two divergence times (τ_1 and τ_2). The parameters Ψ_1 and Ψ_2 are the number of taxon pairs that split at times τ_1 and τ_2 , respectively. (a) Four mammals (recent event), (b) two mammals (older event), (c) one reptile (recent event) and (d) five reptiles (older event).

(c) Hypothesis testing

We use the Bayes factor (Kass & Raftery 1995) to compare posterior support for competing models (simultaneous H_1 and variable divergence times H_2) while accounting for prior support for either model. To calculate Bayes factors, we represent these alternative models as two arbitrary partitions of hyper-parameter space, such that $H_1 = (\Omega < 0.05)$ and $H_2 = (\Omega \geq 0.05)$.

3. RESULTS

The ABC analysis of six mammals and six reptiles indicates that the data are most consistent with two temporally displaced divergence events. For the mammals, the estimate of $\Psi(1.39)$ indicates that one or two divergence times are nearly equally probable. However, the values obtained for $\Omega(0.30)$, and its corresponding Bayes factor (0.07), provide strong evidence supporting multiple divergence times in mammals (figure 1). For reptiles, the estimate of $\Psi(2.11)$ and $\Omega(0.15)$ (figure 1) indicate multiple divergence times, and this is moderately supported by a Bayes factor of 0.25. Although these Bayes factors are based on the hyper-parametric threshold of $\Omega = 0.05$, using Ω thresholds of 0.1 and 0.01 yielded similar Bayes factor support ranging from 0.02 to 0.52 in mammals and 0.18 to 0.40 in reptiles. Although these results are likely to be sensitive to the prior of τ used ($\tau_{\max} = 10.0$), estimates based on simulations have shown that overall conclusions based on hyper-parameter estimates rarely change when τ_{\max} varies from 5.0 to 10.0.

We ran the ABC model conditional on there being two divergence times ($\Psi = 2$) to obtain estimates on τ_1 , the recent divergence time, τ_2 , the more ancient divergence time and the number of taxon pairs that diverged at these two respective times (Ψ_1 and Ψ_2). This suggested that two mammals (*Ammospermophilus leucurus* and *Chaetodipus arenarius*) and five reptiles (*Uta stansburiana*, *Phrynosoma coronatum*, *Callisaurus draconoides*, *Pituophis catenifer* and *Sceloporus zosteromus*) diverged approximately 2.3–15.3 Myr ago when assuming a broad spectrum of divergence rates (figure 2). A recent divergence at approximately 0.6–3.4 Myr ago is supported for the remaining reptile (*Trimorphodon biscutatus*) and mammals (*Chaetodipus baileyi*, *Dipodomys merriami*, *Peromyscus eremicus* and *Thomomys bottae*; figure 2). Although rates are likely to vary between the two taxonomic groups, it is striking that both groups yield two similar divergence time estimates if one naively assumes equal rates. Furthermore, if rate variation within the two groups were causing signatures of multiple divergence events, we would not expect the same pattern of temporal discordance within both groups.

4. DISCUSSION

As a consequence of focusing on the population-level genealogical relationships of organisms across landscapes, studies of comparative phylogeography can

reveal cryptic patterns of vicariance that are invisible to historical biogeographic approaches based solely on taxonomy (Riddle *et al.* 2000a). The paradigm under the traditional approach is to accept a shared biogeographic history as the most parsimonious explanation for concordant patterns of geographical subdivision, or conversely, to assume that unequal divergence times implies multiple divergence events. As advocated in the nascent field of statistical phylogeography, comparative phylogeographic inference requires hypothesis testing with statistical models that incorporate variance in demographic parameters that strongly influence gene-tree coalescent times (Rosenberg & Nordborg 2002; Knowles 2004). By modelling uncertainty into the inherent demographic variance across species with a hierarchical Bayesian model, we have quantified multi-species concordance across the mid-peninsula of Baja California.

The traditional view of a single seaway is insufficient to explain the two episodes of diversification at the mid-peninsula of Baja California and provides an overly simplistic view of evolutionary history. Although marine incursions are supported by geological data (Holt *et al.* 2000), they probably never submerged the Gulf Escarpment, and therefore are unlikely to have acted as a complete barrier to gene flow. Major episodes of volcanism from Middle to Late Miocene to Holocene have produced more than 2500 km² of igneous rocks stretching from the Sea of Cortéz to the Pacific Coast (Sawlan & Smith 1984; Conly *et al.* 2005). If a geological explanation is sought for the mid-peninsular divergences, then it is possible that the combined forces of volcanism and marine incursions created the physical barriers necessary for population subdivision. Alternatively, a strong ecological and climatic gradient occurs at the mid-peninsula and limits the distribution of some species (Grismer 1994). Thus, the strength of adaptive divergence appears to affect species differentially at the mid-peninsula, and this might have resulted in the observed differences in mtDNA divergences apart from the coalescent model that we explicitly incorporate (Edwards & Beerli 2000).

We thank B. Riddle, L. Alexander, T. Devitt, J. Rodriguez-Robles, J. Whorley and A. Lilia Trujano-Alvarez for supplying their datasets; R. Murphy and B. Hollingsworth for tissue samples; B. Hausback and J. Crews for discussion of Baja geology; and J. McGuire, R. Murphy, J. Patton, D. Wake and three anonymous reviewers for their useful comments. This research was funded by a NSFDDIG to A.D.L. (DEB-0508929) and an NSF postdoctoral fellowship in interdisciplinary informatics to M.J.H. (DEB-0305966).

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