

# Spatial and temporal arrival patterns of Madagascar's vertebrate fauna explained by distance, ocean currents, and ancestor type

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**How, when, and from where Madagascar's vertebrates arrived on the island is poorly known, and a comprehensive explanation for the distribution of its organisms has yet to emerge. We begin to break that impasse by analyzing vertebrate arrival patterns implied by currently existing taxa. For each of 81 clades, we compiled arrival date, source, and ancestor type (obligate freshwater, terrestrial, facultative swimmer, or volant). We analyzed changes in arrival rates, with and without adjusting for clade extinction. Probability of successful transoceanic dispersal is negatively correlated with distance traveled and influenced by ocean currents and ancestor type. Obligate rafters show a decrease in probability of successful transoceanic dispersal from the Paleocene onward, reaching the lowest levels after the mid-Miocene. This finding is consistent with a paleoceanographic model [Ali JR, Huber M (2010) *Nature* 463:653–656] that predicts Early Cenozoic surface currents periodically conducive to rafting or swimming from Africa, followed by a reconfiguration to present-day flow 15–20 million years ago that significantly diminished the ability for transoceanic dispersal to Madagascar from the adjacent mainland.**

endemism | phylogenetics | biogeography | evolutionary history | animal distributions

Madagascar's extant vertebrate fauna exhibits high levels of species endemism, yet, for certain groups, is relatively species-poor. Madagascar is also taxonomically imbalanced in that it is not typically "African" (1, 2), as might be expected if most of its ancestors dispersed over a land bridge across the Mozambique Channel or used several intervening islands in a stepping-stone chain facilitated by past lower sea levels (3). Although a few groups appear to be stranded relicts, resulting from Madagascar's shared plate tectonic history with Gondwana (4, 5), for most clades current evidence indicates that the basal stocks arrived after the island was geographically isolated, thus refuting a vicariance model for these organisms.

Currently, the most accepted explanation is that ancestors of most extant Malagasy vertebrate groups rafted, swam, or flew to Madagascar from Africa across the Mozambique Channel during the Cenozoic (6–12). Unfortunately, Madagascar's fossil record of terrestrial vertebrates is restricted to the Late Permian, Triassic, Early–Middle Jurassic, Late Cretaceous (13, 14), and Late Quaternary (extending back only ~80,000 y) (15). As such, this record sheds little light on the critical interval, the Tertiary, when the ancestral stocks of many extant clades are thought to have arrived.

This article analyzes phylogenetic and biogeographic patterns for Quaternary (including extant) Malagasy vertebrate groups within the context of major prevailing geologic and oceanographic conditions throughout the Mesozoic and Cenozoic to provide insights into the mechanisms that resulted in their current existence on the island. We define vertebrate "groups" as Madagascar-endemic clades, each presumed to be descended from a single successful colonization event. Most are families, although other taxonomic ranks (e.g., orders, superfamilies, subfamilies, genera, and species)

are included. We ask whether observed rates of arrival of clade ancestors changed through time and, if so, whether they relate to the position of Madagascar relative to other landmasses, dispersal ability, or geographic source of the colonizers, prevailing ocean currents, or some or all of these factors in combination. We predict that: (i) dispersal ability should affect the probability of arrival more in the Cenozoic than the Mesozoic, because only during the last 20–25 Myr of the 185-Myr long Mesozoic, but during the entire Cenozoic, Madagascar was isolated in the Indian Ocean, and any colonizers would have had to arrive via transoceanic dispersal (flying, swimming, or rafting); (ii) within the Cenozoic, because of proximity, transoceanic dispersal from Africa should be more common than dispersal from Asia; (iii) within the Cenozoic, transoceanic dispersal for obligatory rafters should be more common when surface flows were more conducive to rafting (i.e., during the Paleogene and earliest Neogene (9)); and (iv) assuming some independence of prevailing winds, storm tracks, and ocean currents, volant species should be less affected by ocean current direction than swimmers and terrestrial rafters. We used two databases to test these predictions. The first database was compiled from the biogeographic literature on extant and recently extinct Malagasy vertebrate clades (Table S1). For each of 81 Late Quaternary vertebrate clades, we established arrival date, source, and ancestor type (obligatory freshwater, terrestrial, facultative swimmer, or volant). The second database incorporated new divergence dates from the recent time-tree analysis by Crottini et al. (16) (see *Materials and Methods* for details). In addition, we collected relevant geological, geophysical, and oceanographic information and used this information to construct the temporal units we wanted to compare.

The number of vertebrate clades present on Madagascar during the Quaternary (excluding those introduced, deliberately or inadvertently, by humans) would have depended on (i) vertebrate clade survival across the K–T boundary, (ii) rates of colonization during the Cenozoic, and (iii) rates of clade extinction. Some vertebrate groups may have successfully colonized Madagascar during the Cenozoic but then succumbed to extinction without being represented in the fossil record. In the absence of fossil evidence, we cannot know the actual rates of clade arrival or extinction through most of the Cenozoic. However, we can test the null hypothesis that background extinction had no effect in shaping the modern (Quaternary) vertebrate assemblage (i.e., there is no relationship between the geological age of clades and their probability of Quaternary representation). If in fact we must reject this null hypothesis, we can still compare arrival rates across time intervals by modeling bound-

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any conditions; that is, the extent to which arrivals that are invisible because of background extinction might influence our inferences. In this article, we do both. We note, however, that most of the comparisons we make are of states (dispersal type, geographic source, colonizer type) within single time intervals, which can be explored without considering missing arrivals and extinctions, and which we do indeed treat without any adjustment for missing data.

## Results

The results of our statistical analyses of patterns of colonization are provided in Fig. 1, Tables 1–3, and Tables S2 (our literature-derived database) and S3 [the same database modified to incorporate recent data derived from Crottini et al. (16)]. There is complete concordance between the two, suggesting that our inferences are robust. Specific values reported below pertain to Table S2. None of the results presented in Tables S2 or S3 entail adjustment for missing data.

During most of the Mesozoic (all except the last 20–25 Myr), when transoceanic dispersal was not required for either emigration or immigration, there is no evidence that arrival rates for ancestors that we consider dispersal-advantaged (volant species or facultative swimmers) were higher than those for dispersal-disadvantaged (terrestrial or obligate freshwater species) ancestors. In fact, the opposite is true. In contrast, during the Cenozoic, when transoceanic dispersal was the only mode of arrival, the arrival rate for dispersal-advantaged taxa was more than three times that of dispersal-disadvantaged taxa (0.81/Myr vs. 0.23/Myr;  $P < 0.001$ ) (Table S2). Thus, our first prediction—that dispersal advantage should be more important in the Cenozoic than the Mesozoic—is supported.

Our second prediction—that transoceanic rafting from Africa should be more common than rafting from Asia during the Cenozoic—is also supported. This source difference is highly significant for terrestrial taxa ( $P = 0.005$ ), weakly significant for volant taxa ( $P = 0.04$ ), and nearly significant for facultative swimmers ( $P = 0.1$ ), despite their very low numbers (Table S2). Terrestrial taxa and facultative swimmers arrive from Africa 5–6.5 times more often than from Asia; for volant taxa, arriving from Africa is twice as likely.

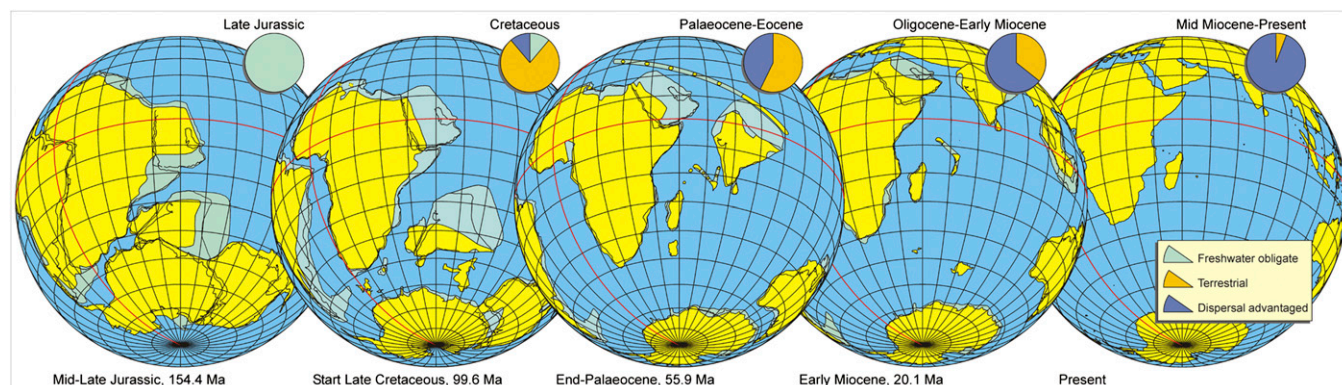
Our third prediction—that, during the Cenozoic, obligate rafters (terrestrial taxa) should have arrived in greater numbers when ocean currents were more conducive to rafting, during the Paleogene and earliest Neogene, and that a tipping point should have occurred in the mid-Miocene, coinciding with the shift in ocean surface current direction (1)—is not supported. Contrary to expectations, dispersal-disadvantaged taxa show no significant change in arrival rate from before to after the mid-Miocene ( $P = 0.95$ ). However, dispersal-advantaged taxa show a highly significant increase in arrival rate after the mid-Miocene, when prevailing currents shifted to favor Asia. This shift holds for both facultative swimmers ( $P < 0.001$ ) and volant taxa ( $P < 0.001$ ). Overall arrival rates for taxa from Africa ( $P < 0.001$ ) and Asia ( $P = 0.002$ ) both increase significantly after the shift in current direction. The most

striking difference is not a change in source but a change in colonizer type: volant taxa dominate arrivals after the shift in ocean current ( $P < 0.001$ ) but not before ( $P = 0.71$ ), supporting our fourth prediction that volant species should be less affected by ocean current direction than obligatory rafters (Table S2).

Of the above predictions, only the third is potentially affected by background clade extinction, because it compares arrival rates over time (rather than within single time intervals). If we make no adjustment for background clade extinction or “invisible” arrivals, we are implicitly assuming that the probability of observing a clade in the Late Quaternary (including the present day) is unrelated to its arrival time (i.e., there is no effect of extinction). However, this assumption can be tested; if the probability of clade extinction at any point in time has not changed significantly over time, then a greater proportion of the clades that arrived early should have also disappeared, resulting in a biased representation of young clades in the Quaternary.

In fact, this prediction holds. A  $\chi^2$  test of the relationship between clade age and Quaternary representation confirms our suspicion of an important clade extinction effect, not merely at the K–T boundary, but through the Cenozoic (Table 1). There are highly significant differences in arrival rate through time, and the Quaternary (including extant) fauna has a disproportionate representation of young clades. Again, there is no inferential difference between results derived from our original database ( $P < 0.001$ ), and that modified by Crottini et al. ( $P < 0.001$ ) (Table 1) (16). The apparent increase in arrival rate over time is consistent and striking.

This result implies that we cannot compare arrival rates across time intervals without considering “invisible” arrivals and their implied background extinction rates. We are interested in temporal changes in arrival rates for different vertebrate groups during the Cenozoic; testing our third prediction depends on our ability to decipher them. The simplest “adjustment” that we can make is to assume that the recent past provides a good model for estimating average arrival rates in the more distant past (a uniformitarian assumption), and that the lower apparent arrival rates for the Paleogene and earliest Neogene are artifacts of extinction. Thus, we assume average vertebrate arrival rates of 2.33/Myr throughout the Cenozoic, but we apportion them in each time interval according to observed differences in ancestor type. With the Cenozoic data adjusted in this manner for background extinction bias, an interesting temporal pattern emerges. Specifically, our third prediction (that obligatory rafters arrived in greater numbers when ocean currents were more conducive to rafting) is supported. Terrestrial (dispersal-disadvantaged) species exhibit the strongest temporal shift, having been most likely to arrive in the Paleocene–Eocene (at a rate of 1.33/Myr); that probability decreased during the Oligocene to mid-Miocene (0.85/Myr), and markedly so again during the mid-Miocene to present (0.13/Myr) (Table 2). Dispersal-advantaged taxa (most of which were volant) show the opposite trend, increasing significantly over time (from 1.01 arrivals per million years in the Paleocene–Eocene to 2.20 arrivals per million



**Fig. 1.** Maps showing changing landmass configurations and patterns of vertebrate appearance in or colonization of Madagascar by time slice and proportion of dominant colonizer types. These data are observed, unadjusted frequencies, converted to percentages.

**Table 1. Observed arrival pattern through time, with values expected under the assumption that arrival rates were, on average, the same through time, and with  $\chi^2$  test of the significance of arrival rate differences over time**

Epoch	Duration (Myr)	Observed $n$	Expected $n$	Arrival rate (arrivals/Myr)	$\chi^2$	$n$	$df$	$P$
Original database								
Mid-Miocene to present	15.0	35	7.1	2.33	136.4	76	4	<0.001
Oligocene to mid-Miocene	18.9	14	8.9	0.74				
Paleocene to Eocene	31.6	14	14.9	0.44				
Cretaceous	80.0	9	37.8	0.11				
Late Jurassic	15.7	4	7.3	0.26				
Crottini et al. database (16)								
Mid-Miocene to present	15.0	33	7.1	2.20	124.3	76	4	<0.001
Oligocene to mid-Miocene	18.9	14	8.9	0.74				
Paleocene to Eocene	31.6	18	14.9	0.57				
Cretaceous	80.0	10	37.8	0.13				
Late Jurassic	15.7	1	7.3	0.06				

Categories were chosen to reflect major geologic and oceanographic conditions.

years in the mid-Miocene to present) (Table 2). Because the shift in ocean current direction made successful arrival of terrestrial species increasingly difficult, the relative proportion of dispersal-advantaged to disadvantaged colonizers increased (Fig. 1).

To test the robustness of this inference, we calculated boundary conditions. We know that our third prediction would hold if the actual average successful colonization rates for vertebrates in the Cenozoic were 2.33/Myr or higher. We tested lower successful colonization rates for the period before the mid-Miocene to determine the point at which significance is lost. Strong significance holds for dispersal-advantaged species regardless of arrival rate. A significant result also holds for dispersal-disadvantaged species as long as the overall successful colonization rate before the mid-Miocene was 1.3/Myr ( $P = 0.05$ ) or higher. In other words, even if the rate of successful vertebrate colonization from the Paleocene to the mid-Miocene was, on average, only 56% (1.3/2.3) of the rate we observe from the mid-Miocene to the present (before human arrival), our third prediction would hold. In fact, given that ocean currents were more conducive to dispersal before the mid-Miocene, it is likely that successful vertebrate colonizations were higher before the mid-Miocene than

afterward; our models are highly conservative. We therefore suggest that our inferences, including confirmation of the third prediction, are robust; they are contextualized in Table 3 (17, 18).

## Discussion

Although recent research has defended the importance of dispersal in shaping the faunal composition of Madagascar (7, 19–21), and for animal distributions in general (22–25), this study is unique in rigorously testing these ideas. First, we have shown that dispersal ability affected the probability of arrival more in the Cenozoic than in the Mesozoic, likely because, during the entire Cenozoic, Madagascar was fully isolated physically from other landmasses and all arrivals were, of necessity, via transoceanic dispersal. Second, within the Cenozoic, both before and after the mid-Miocene, Africa was the primary source and Asia (including the Indian subcontinent) the secondary source of colonizers. There is considerable evidence that distance is the most important factor for colonization success for terrestrial dispersers; the much greater distance from Asia to Madagascar was relatively prohibitive. Third, transoceanic dispersal for obligatory rafters during the Cenozoic

**Table 2. Arrival pattern during the Cenozoic for dispersal-disadvantaged and dispersal-advantaged taxa, with data adjusted to account for effects of background extinction, assuming average successful colonization rates during the 50.5 Myr before the mid-Miocene comparable to that observed during the past 15 Myr**

Type of ancestor	Time interval	Adjusted $n$ for each time interval	Implied arrival rate (per Myr)	Expected proportion for each time interval	Expected $n$ for each time interval	$\chi^2$	$n$	$df$	$P$
Original database									
Dispersal-disadvantaged	Mid-Miocene to present	2	0.13	0.23	13.8	16.3	60	2	<0.001
	Oligocene to mid-Miocene	16	0.85	0.29	17.4				
	Paleocene to Eocene	42	1.33	0.48	28.2				
Dispersal-advantaged	Mid-Miocene to present	33	2.20	0.23	21.4	9.9	93	2	0.007
	Oligocene to mid-Miocene	28	1.48	0.29	27.0				
	Paleocene to Eocene	32	1.01	0.48	44.6				
Crottini et al. database (16)									
Dispersal-disadvantaged	Mid-Miocene to present	1	0.06	0.23	14.3	21.7	62	2	<0.001
	Oligocene to mid-Miocene	15	0.79	0.29	18.0				
	Paleocene to Eocene	46	1.46	0.48	29.8				
Dispersal-advantaged	Mid-Miocene to present	32	2.13	0.23	19.1	15.4	83	2	<0.001
	Oligocene to mid-Miocene	27	1.43	0.29	24.1				
	Paleocene to Eocene	24	0.76	0.48	39.8				



**Table 3. Timetable for major changes relevant to the geological and biogeographic history of Madagascar**

Date (Myr)	Paleogeographical context	Biogeographic events
8	Increase in intensity of monsoon system.	Ratio of dispersal-advantaged to dispersal-disadvantaged
15	Direction of flow of ocean surface waters now no longer conducive to transoceanic dispersal from Africa to Madagascar. Tibetan Plateau reaches current elevation.	colonizers arriving during the past 15 Myr (but before arrival of humans ~2,500 y ago) is 16:1.
20	At about this time, Madagascar's northern tip begins impinging on the southern equatorial current. It commences a shift in the regional oceanic surface water flow that eventually leads to the modern configuration. It is notable, for it makes Africa to Madagascar over-water dispersal extremely difficult.	From beginning of Oligocene to mid-Miocene, approximately twice as many dispersal-advantaged colonizers arrive as dispersal-disadvantaged taxa. This ratio increases dramatically after shift in prevailing direction of ocean current flow (~20–15 Myr).
23	(Oligocene/Miocene boundary) Monsoon climate of southern Asia and surrounding oceans established.	
35	Indian subcontinent collides with southern Asia, resulting in Himalayan uplift. Abrupt cooling and a major sea-level fall induced by the growth of the ice-sheet on Antarctica marks the Eocene/Oligocene boundary, ~34 Myr.	
40–45	By mid-Eocene, most of Madagascar is north of 30° southern latitude, and thus strongly influenced by the trade winds.	During Paleocene and Eocene (i.e., between 65.5 Myr and 33.9 Myr) dispersal-advantaged and dispersal-disadvantaged colonizers arrive in approximately equal numbers.
57	Northeast corner of India close to southeast Asia.	
65	Ocean separating Indian subcontinent and Madagascar vast. Ocean surface currents conducive to transoceanic transport from Africa to Madagascar (possibly taking ~30 d).	
84	Kerguelen Plateau largely submerged.	Ancestors of some vertebrate groups still represented on Madagascar in Quaternary are believed to have arrived during Cretaceous, between ~145.5 Myr and 65.5 Myr. Major extinction event marks end of Cretaceous. Almost all vertebrate groups in Mesozoic strata of Madagascar are unrepresented in island's Quaternary or extant vertebrate faunas.
88	Madagascar and Indian subcontinent begin separating.	
115–95	Substantial parts of Kerguelen Plateau are emergent, but separated from Indo-Madagascar and Antarctica by deep-water gaps.	
115–112	Any land connection between Madagascar and Antarctica via the Gunnerus Ridge is broken.	
130	Eastern Gondwana begins to breakup with Indo-Madagascar splitting from Antarctica–Australia.	
136	After this time, the spreading between western and eastern Gondwana increases the gap between the two landmasses (it stops at 120–116 Myr).	
165	Western Gondwana (Africa and South America) and Eastern Gondwana (Madagascar, Indian subcontinent, Seychelles, Australia, and Antarctica) begin separating but remain in close proximity.	Some clades of freshwater fish still represented on Madagascar today are believed to have arrived in Late Jurassic, beginning ~161 Myr.

was more common when ocean currents were conducive to rafting. Rafters and swimmers did occasionally colonize Madagascar from Africa against the prevailing current, suggesting some stochasticity in current direction (26, 27); yet, generally, arrivals of terrestrial colonizers were rare after ocean currents in the Mozambique Channel shifted their prevailing direction in the mid-Miocene. Finally, and not unexpectedly, we show that volant species were less affected by ocean current direction than terrestrial species or facultative swimmers; the greater distance from Asia to Madagascar was not prohibitive.

A few additional inferences can be drawn from our data. According to most reconstructions, major freshwater fish groups were well established in Madagascar before the K–T boundary (refs. 28 and 29; but see also ref. 16). The apparent lack of freshwater fish arriving after the Mesozoic underscores a transoceanic dispersal disadvantage far more prohibitive than that which applies to terrestrial (rafting) taxa. It is also possible that the apparent “advantage” for “dispersal-disadvantaged” taxa during the Mesozoic is simply an artifact of persistence; once Madagascar was isolated, these freshwater fish faced no incoming competitors whereas for other groups there was a greater chance of competitive displacement.

Amphibians tend to have low tolerance for marine environments, although salinity tolerance is variable among groups (30), and there is no question that amphibians have crossed marine barriers successfully (21, 31), given their presence on geologically young oceanic islands of volcanic origin (19). However, this understanding does not mean that their mechanism of dispersal would have been swimming. It is far more likely that their ancestors rafted on mats of vegetation, as did terrestrial colonizers.

Facultative swimmers exist in relatively small numbers, suggesting that the ability to swim long distances only rarely confers

dispersal advantage. Madagascar's facultative swimmers include large-bodied reptiles (e.g., crocodiles) and mammals (e.g., hippopotamuses). Their arrival rates are considerably lower than those of volant species, and they arrived more often from Africa than from Asia, suggesting that distance restricted their dispersal ability. A true swimming “advantage” may only apply to very large mammals (e.g., hippopotamuses) that can traverse large distances by virtue of their fat reserves (32), and certain semiaquatic reptiles, such as crocodiles or turtles. Hippopotamuses are known to have arrived well before the arrival of humans (33), but nevertheless in the Neogene, presumably by swimming. Crocodiles are also thought to have arrived recently (34, 35), possibly through two independent dispersal events (36). Washed-up elephant remains on Ile Europa, midway in the Mozambique Channel between Africa and Madagascar, may also indicate a nonsuccessful dispersal event (37). These taxa all derive from the nearest major landmass, Africa.

Some researchers have discounted the likelihood of terrestrial rafters surviving on the open seas, citing solar radiation, lack of water and food, and intense fluctuations in temperature that would elevate physiological stress (38). However, Van Duzer's (39) compilation of historic sightings of terrestrial vertebrates on floating islands bears testimony to the relative frequency of such occurrences, and to conditions under which even physiologically challenged species may survive long oceanic transport. In recent history, floating islands (up to 100 m across) have been reported at sea up to 240 km from their places of origination, some housing large, food-bearing trees and freshwater pockets. The frequency of such sightings argues strongly that this mechanism of transport cannot be summarily dismissed (40).

Species with the greatest dispersal advantage are volant. Oceanic crossings by birds and bats have been more frequent than crossings by either terrestrial or freshwater vertebrates. Madagascar has 44 recognized bat species, reflecting at least 24 independent colonization events (41); of the eight bat families occurring on the island, only one is endemic. Volant species show relatively low African source bias, suggesting they are not strongly influenced by ocean current direction. Of greater relevance to volant species are prevailing wind direction (42) and the pattern and frequency of storms. Volant taxa of Asian origin may have used stepping stones, such as India, or the Seychelles, Andaman, or Mascarene islands.

Madagascar today experiences easterly on-shore winds, being located squarely within the trade-wind zone (which extends from 30° N to 30° S, ~5° south of Madagascar's current southernmost tip); our best models of Mesozoic and Cenozoic coastlines show that Madagascar was already well within the southeast trade-wind zone by the mid-Eocene, and remained there throughout the rest of the Cenozoic (43) (Fig. 2). Trade winds would have aided the transfer of volant animals from the center or eastern tropical Indian Ocean, including Australia, southeast Asia, and the Indian subcontinent.

In the austral summer, the southwest Indian Ocean region is affected by cyclones and large tropical storms (44, 45) and, as with other similarly situated regions (e.g., Caribbean, Gulf and Atlantic coasts, southeast Asia–northwest Pacific), it would appear that such weather systems can move (and are known to have moved) birds and bats far from their normal distributions, in some cases hundreds of kilometers (46–50). Hence, it is clear that, for flying taxa, distance is not the sole controlling factor.

Other factors likely influenced the dispersal success of birds and bats, including their sociality and reproductive adaptations. The fact that some bats are capable of sperm storage may have given them an increased probability of successfully colonizing and diversifying (51). Animals living in groups, as do many birds and bats, have a greater probability of being carried off with conspecifics, thus increasing the chance of mating and, thereby, successful colonization. An increase in storm frequency likely occurred with the emergence of the monsoon climate of southeast Asia and Madagascar during the past 20 Myr (Table 3) (52). Recent evidence suggests that some

bats are highly capable dispersers; *Mops midas* seems to have repeatedly moved between Africa and Madagascar (53). Finally, changes in the availability of dispersers through time may have also affected changes in dispersal frequency over time; for example, some volant groups (e.g., passerine birds) experienced diversifications after the mid-Miocene (54) that could have increased their subsequent likelihood of colonization.

However, other factors for which we were unable to account may have affected Madagascar's colonization history. Changes through time in the availability of dispersers of different body sizes or physiological adaptations may have affected the probability of successful transoceanic dispersal. Small body size should benefit volant (flying) and terrestrial (rafting) species, but not facultative swimmers, for example.

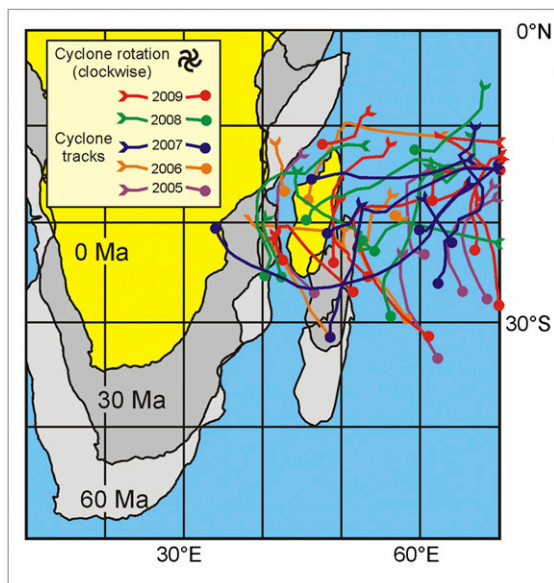
Nevertheless, our results strongly support the importance of transoceanic dispersal by wind and water as the vehicles whereby most extant vertebrates endemic to Madagascar became established. Prior authors have defended transoceanic dispersal to the island on the basis of the phylogenetic affinities and molecular divergence times of particular taxa (6–9, 19, 20, 22–24, 55). Our argument derives instead from variation in observed colonization patterns: dispersal-advantaged colonizers outnumber dispersal-disadvantaged colonizers during the Cenozoic but not during the Mesozoic; terrestrial species were more likely to arrive when currents were more conducive to transoceanic dispersal; and terrestrial colonizers (unlike volant species) arrived virtually exclusively from the nearest landmass (Africa) during the Cenozoic. Finally, we suggest that the apparent increase in successful colonization rates through the Cenozoic can best be interpreted as an artifact of clade extinction. If we are correct with regard to this latter point, then future discoveries of vertebrate fossils from the Paleogene should include a significant number of clades unrelated to those represented in Madagascar's Mesozoic, subfossil Quaternary, or extant vertebrate faunas.

## Materials and Methods

Data reflecting our understanding of the biogeographic history of the extant Malagasy vertebrate fauna and key geological, geophysical, and oceanographic information were compiled from the literature (Table S1). For each of 81 clades represented in the extant or Quaternary "subfossil" fauna, we scored: (i) time of arrival (Late Jurassic, Cretaceous, Paleocene–Eocene, Oligocene to early Miocene, mid-Miocene to present) and source area (Gondwana, Indo–Madagascar, Africa, India/southeast Asia, Madagascar); (ii) ancestor type (obligate freshwater, terrestrial, facultative swimmer, volant); (iii) for Cenozoic arrivals, prevailing ocean current direction at time of arrival, based on paleoceanographic modeling; and (iv) dispersal ability (advantaged, disadvantaged). Estimates of time and origin of clade arrival were drawn from the literature, ideally from dated molecular phylogenies combined with cladograms based on standard morphological data that can also integrate fossil taxa. Arrival counts per time interval were converted to observed arrival rates (number/million years), which were analyzed for samples pooled by ancestor type, source, and so forth. We also constructed a second database that incorporated recent divergence dates from the recent time-tree analysis by Crottini et al. (16).

We used the  $\chi^2$  function in Minitab v15 to compare observed arrival rates;  $\chi^2$  allows the use of a hypothesized set of rates (counts per time interval) to calculate an expected set of counts and compare those to observed rates. We used standard null hypotheses to generate rates driving arrival and compared expected counts dictated by our hypothesized rates to actual observed counts. All such calculations (Tables S2 and S3, on each of the two databases) were executed without adjustments for extinction.

Null hypotheses assuming (i) equivalent arrival rates for two "states" or (ii) uniform average arrival rates for single states through time, were used to generate expected counts, which we then compared with observed counts. For example, assuming a particular arrival rate for a group of colonizers of a particular type across different periods of time, the expected arrival rates for each period become our total  $n$  of arrivals divided by the total time, and the expected arrival counts for each period become proportional to the time represented by each period. Alternatively, in comparing, for example, volant and terrestrial colonizations during a single time period, the expected arrival rates under the null hypothesis of no difference by animal type is half the total  $n$  of arrivals for each animal type, divided by the period. Observed counts are, of course, constrained not merely by our selections (e.g., Cenozoic only) but by missing data (e.g., missing arrival time or missing source for particular colonization events) and thus will not be identical for all tests.



**Fig. 2.** Map showing the northward drift of Africa and Madagascar from the Paleocene (60 Ma), Oligocene (30 Ma), and present day (0 Ma); Madagascar has moved from outside to within the southerly limit of the southeast trade winds (~30° S). Superimposed on the map are cyclone tracks for 2005–2009, showing the potential influence of tropical storms in aiding transoceanic dispersal ("fish-tail" indicates either the initiation point or the position where the storm enters the map area; dot indicates the end point).

When drawing inferences about the past from vertebrate clades represented in the present or very recent past, we should expect undetected background extinctions to bias results. Background extinction rates should not influence tests of whether particular colonizer types were more prevalent than others during a particular time interval, but they may impact inferences regarding temporal changes in arrival rates for particular types. Fortunately, we can apply simple tests to determine whether in fact extinction has played a significant role, and we can apply simple models to make data adjustments that, in effect, "correct" the data for expected missing clade counts. The farther back in time, the more likely the extant counts will be "missing" cases of lineage arrivals and lineage extinctions during that time period. This distinction is important only when comparisons are made of arrival rates over time (our "Prediction 3").

The three time periods of the last 65.5 Myr that we analyzed comprise 31.6, 18.9, and 15 Myr respectively, and yielded 14, 14, and 35 known vertebrate arrivals. We adopted the most recent time period of 15 Myr with its 35 arrivals as our baseline. From this information we infer an average arrival rate of 2.33 successful colonizers per million years. Applied to the whole 65.5 Myr, we estimate a total of 153 successful vertebrate colonizations during the

Cenozoic; because we observe only 63 in the extant and recently extinct vertebrate fauna, 90 clades are presumed to have gone extinct.

We then used the arrival-rate discrepancies from 2.33 for the Paleocene to Eocene and the Oligocene to mid-Miocene to allocate the 90 in a 60/30 split. We used the observed animal type (advantaged/disadvantaged) frequencies for each of these time periods to split the added counts into their appropriate cells. Finally, we tested arrival rates lower than 2.33, to determine the rate below which our statistical inferences would change. Higher average arrival rates would not alter our statistical inferences; rather, they would increase our confidence in these inferences.

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