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ORIGINAL ARTICLE

Did lemurs have sweepstake tickets? An exploration of Simpson's model for the colonization of Madagascar by mammals

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ABSTRACT

Aim To investigate the validity of Simpson's model of sweepstakes dispersal, particularly as it applies to the colonization of Madagascar by African mammals. We chose lemurs as a classic case.

Location The East African coast, the Mozambique Channel and Madagascar.

Methods First, we investigated the assumptions underlying Simpson's statistical model as it relates to dispersal events. Second, we modelled the fate of a natural raft carrying one or several migrating mammals under a range of environmental conditions: in the absence of winds or currents, in the presence of winds and currents, and with and without a sail. Finally, we investigated the possibility of an animal being transported across the Mozambique Channel by an extreme climatic event like a tornado or a cyclone.

Results Our investigations show that Simpson's assumptions are consistently violated when applied to scenarios of over-water dispersal by mammals. We suggest that a simple binomial probability model is an inappropriate basis for extrapolating the likelihood of dispersal events. One possible alternative is to use a geometric probability model. Our estimates of current and wind trajectories show that the most likely fate for a raft emerging from an estuary on the east coast of Africa is to follow the Mozambique current and become beached back on the African coast. Given prevailing winds and currents, transport from Madagascar to Africa is very much more likely than the reverse process. Freak transport by means of a hurricane or tornado is even less likely than rafting for mammals.

Main conclusions Our models suggest that the scenario of sweepstakes dispersal that currently enjoys wide support is not valid at either the theoretical or the applied level when applied to the hypothetical invasion of Madagascar by African mammals. Alternative explanations should be sought.

Keywords

Lemurs, Madagascar, mammals, Mozambique Channel, rafting, Simpson, sweepstakes dispersal, waifs.

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INTRODUCTION

The fossil records of the living orders of mammals do not extend much earlier than the latest Cretaceous/early Palaeocene (Alroy, 1999; Foote *et al.*, 1999). If this evidence indeed reflects the time of origin of the orders, rather than indicating the inadequacy of the fossil record (Martin, 1993; Hedges *et al.*, 1996; Arnason *et al.*, 1998; Kumar & Hedges, 1998; Penny *et al.*, 1999; Eizirik *et al.*, 2001; Madsen *et al.*, 2001; Murphy *et al.*, 2001; Tavaré *et al.*, 2002), then the radiation and dispersal of the extant mammals post-dates the major episodes of continental movement that marked the break-up of the Gondwana supercontinent. Thus, explanations of mammalian biogeography must be constructed against an essentially 'fixed continents' background, and require dispersal mechanisms like land bridges and 'sweepstakes' oceanic crossings in much the same way as in the work of pioneering biogeographers like A.R. Wallace and G.G. Simpson. As more

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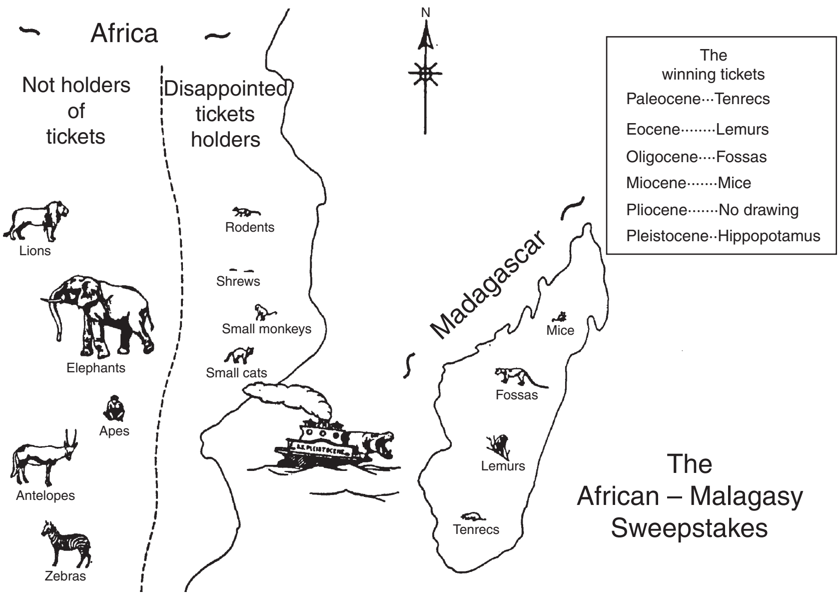

Figure 1 Simpson's (1940) diagram to illustrate the sweepstakes model for the mammalian invasion of Madagascar.

information on sea-floor topography has become available, many of the early scenarios regarding land bridges and lost continents have become untenable, and biogeographers have fallen back on the 'sweepstakes' model proposed by Simpson (1940, 1952). In this interpretation, dispersal events that may be improbable within any limited time period become more probable given vast periods of geological time, although dispersal will always be more likely for some kinds of organisms than for others.

A particularly interesting case, which has intrigued and frustrated biogeographers since the birth of the science (see e.g. Wallace, 1892; Simpson, 1940; Walker, 1972; Gingerich, 1975; Simons, 1976; Masters *et al.*, 1995; Rage, 1996, 2003; Sampson *et al.*, 1998; de Wit, 2003), concerns Madagascar. The rending of Madagascar from the east coast of Africa occurred as part of the initial sundering of western and eastern Gondwana, and was initiated around 170 Ma (Rabinowitz *et al.*, 1983; Reeves & de Wit, 2000; de Wit, 2003). Madagascar was displaced southwards, passing close to the African coast at about 140 Ma (Reeves & de Wit, 2000), before it came to occupy its present position, approximately 430 km east of Mozambique, between 120 and 130 Ma (Rabinowitz *et al.*, 1983; Coffin & Rabinowitz, 1988; Torsvik *et al.*, 1998). Thus, over the entire period encompassing the origin and radiation of the modern mammalian orders, the distance between Africa and Madagascar has not undergone any significant change. Madagascar's living and recently extinct mammal fauna comprises a highly selective sampling of orders that occur on the African continent, and these orders appear to have colonized the island continent at different times (see below). Hence, this fauna became the paradigm for Simpson's sweepstakes model (Fig. 1).

The extant mammalian fauna of Madagascar includes representatives of five orders: bats (Chiroptera), tenrecs (Afrosoricida), rats and mice (Rodentia), small to medium-sized carnivores (Carnivora) and lemurs (Primates). In addition, fossilized remains representing two other orders have been discovered in relatively recent sediments: three dwarf hippopotamus species (Holocene, order Artiodactyla) and two species of 'false aardvarks' (Quaternary, order Bibymalagasia). The bats show clear evidence of relatively recent migration from founder populations in Africa, as might be expected (Garbutt, 1999). The dwarf hippopotamus species apparently arrived on the island relatively recently by means of three independent colonizations (Garbutt, 1999). No proposals have been made regarding either the timing or the manner of the invasion of Madagascar by pseudo-aardvarks.

The biogeographical history of the four extant non-volant orders has received considerably more attention. It is common cause among students of primate evolution (e.g. Martin, 1972; Walker, 1972; Yoder *et al.*, 1996; Krause *et al.*, 1997; Kappeler, 2000; Sieffert *et al.*, 2003; Roos *et al.*, 2004) that the living lemur radiation is the result of a single invasion of Madagascar from the African mainland, most likely by rafting. Molecular estimations of the date of this event range from as early as *c.* 80 Ma (Sarich & Cronin, 1976; Roos *et al.*, 2004; Yoder & Yang, 2004) to as recently as *c.* 50 Ma (Porter *et al.*, 1997), with a mean of 58.7 Ma (calculated from data presented by Yoder *et al.*, 1996; Porter *et al.*, 1997; Yoder, 1997; Arnason *et al.*, 1998; Goodman *et al.*, 1998; Roos *et al.*, 2004; Yoder & Yang, 2004). The rather limited carnivore radiation, consisting of 'mongooses', the Malagasy 'civet' and the fossa, has also been identified as descended from a single over-water immigration event from Africa (Yoder *et al.*, 2003), estimated to have occurred at around the Oligocene/Miocene boundary or even later, 24–18 Ma (Veron & Catzeflis, 1993; Yoder *et al.*, 2003). The tenrec radiation appears to have had a more complex history. Sister-taxon relationships have been mooted between the Malagasy genus *Limnogale* and the potamogalines of Africa (Asher, 1999), and the Malagasy genus *Geogale* and the extinct genus *Parageogale* from the early Miocene of East

Africa (Butler, 1985; McKenna & Bell, 1997), indicating multiple crossings of the Mozambique Channel for this group. Douady *et al.* (2002) estimated that the divergence between the African and Malagasy tenrecs occurred between 53 and 37 Ma. Finally, like the lemurs and the carnivores, the nine endemic genera of nesomyine rodents are believed to be the descendants of a single colonization event (Dubois *et al.*, 1996; Jansa *et al.*, 1999). However, in the reconstruction of Jansa *et al.* (1999), the colonizers came from Asia, not Africa, and went on to invade the African mainland once they had become established on Madagascar.

At least one crossing of the Mozambique Channel seems inescapable, therefore, for lemurs, carnivores and tenrecs. But just how likely is such a crossing, even given the time period of *c.* 20 to 80 Myr indicated by phylogenetic studies? In this paper we explore Simpson's (1940, 1952) explanation for the mammalian colonization of Madagascar, using a hypothetical ancestral lemur (or group of lemurs) as a test case. We approach the exploration from two angles. First, we investigate the statistical model he proposed, and find that it is flawed. Second, we model the fate of a floating island raft, with and without a 'sail', venturing out of an estuary on the eastern coastline of Africa into the Mozambique Channel, in both the absence and the presence of ocean currents and under varying weather conditions, and give an idea of the probabilities associated with each parameter set. We show that Simpson's model has serious shortcomings, both from a practical and a theoretical perspective.

THE MODELS

The statistical basis of Simpson's sweepstakes model

Simpson's (1952) sweepstakes model was based on the binomial expression

$$(p+q)^n \tag{1}$$

(where $q = 1 - p =$ failure), and states simply that a trial which is repeated indefinitely (n very large) will yield a probability of success that approaches 1 (i.e. a certain event). In a binomial process, two assumptions must be satisfied:

1. There are n independent trials, and n is fixed.

2. Each trial has two possible outcomes: success [Pr(success) $= p$] or failure [Pr(failure) $= 1 - p = q$]. The probability (Pr) of success from trial to trial is constant.

From this, the number of successes (X) in n trials will follow a binomial distribution.

Simpson examined two binomial models:

Model A:

1. $n =$ size of the population, and each member of the population represents a trial.

2. $p =$ Pr(successful dispersal of a single individual).

Using this model, Simpson showed that in a population of 1,000,000, and with the probability that a single individual will cross the barrier equal to 1 in 1,000,000, the chance that at least one individual will cross the barrier is 0.63 (i.e. almost 2 in 3).

Model B:

1. $n =$ number of years involved, and each year represent a trial.

2. $p =$ Pr(dispersal from a given population in any year).

Simpson then showed that during the course of 1,000,000 years, with dispersal occurring more than once, the probability of success is also 0.63 (i.e., a likelihood of two out of three).

We believe that both of Simpson's models are misleading.

Simpson's model A

First, the size of the population (n) cannot be fixed, and thus the probability of an individual crossing successfully is not constant from trial to trial. Natural fluctuations in population size affect the probability of dispersal of individuals. For the binomial model to hold, successive trials must be performed under conditions identical to the first (Stuart & Ord, 2000), and in terms of sweepstakes dispersal this is an unrealistic assumption.

Second, Simpson uses a single population of 1,000,000 individuals. This is also unrealistic. The lemurs most likely to be involved in dispersal are those living near a river mouth, or along the coast. It is less likely that inland lemurs would travel both over land and then across the water barrier. For example, if we assume the lemur population in Africa is N, of which M live 'near the raft', the sample size M will be much smaller than N.

Third, successful colonization also implies that lemurs must land within reach of one another, and within one another's life spans, in order to breed. This would require a survival window of < 25 years (the maximum life span of a fertile lemur) or the involvement of a pregnant female – as mentioned later.

To quantify these factors into a single probability value is difficult, and could probably only be done subjectively.

Simpson's model B

First, in this model, n represents the number of years during which trials can take place, and each year represents a trial. For the binomial model to apply, the years must be independent. We assume that for 'normal' years (i.e. when no extreme event occurs to facilitate a crossing) the years are independent, but once an extreme event does occur it will have an influence on subsequent years such that they are no longer independent.

Second, molecular clock estimations indicate that the lemur dispersal took place some time between 80 and 50 Ma, providing a window of opportunity of *c.* 30 Myr. A valid question then would be whether 30 million trials represents a fixed number or whether it can be considered to approach infinity? The number of years is in effect unknown, and therefore not fixed.

Third, the assumption of constant probability of success from year to year is unlikely to be valid. It is more accurate to say that the probability of success in each trial approaches 0 ($p \to 0$ and $n \to \infty$).

Fourth, the 'sweepstake' process should be discontinued once a dispersal event has taken place. As our dispersal models show (see below), dispersal from Madagascar to Africa is much more likely than from Africa to Madagascar. What prevented lemurs from returning to Africa?

Based on the violation of the assumptions of the binomial model, as outlined above, we suggest that the Simpson's sweepstake model should be disregarded. Instead other possible probability models should be explored. One such model is a geometric probability, based on at least five more realistic assumptions for the problem of lemur colonization:

1. The probability that an individual lemur will cross the water barrier on its own and then find a lemur in Madagascar of the opposite sex within his/her life span is a near-impossible event [i.e. what is the probability that a second lemur (of the opposite sex) will cross the water within 25 years of the first lemur, and that it will be able to locate the first lemur in Madagascar?]. Successful colonization is much more likely if a group of lemurs migrates on the same raft or 'floating island' (Houle, 1998, 1999). However, this probability remains low, as shown later in this paper ($p \to 0$).

2. The available molecular evidence (Yoder *et al.*, 1996) implies that the lemur colonization was a single event. Hence, we must assume that once a successful dispersal event occurred the sweepstakes process ceased.

3. If we define the random variable, X, as the total number of trials per unit time (years) (failures; unsuccessful dispersal) before a successful dispersal, the only thing we know about X, is that $X < 30$ million.

4. The probability of dispersal from year to year is not constant, and for the ith year it is given as p_i. This probability, although different from year to year, is still a very low probability. The probability of a failure, or no dispersal is $1 - p_i = q_i$.

5. The years before a sweepstake event (i.e. no dispersal, X years) are independent.

Based on the above assumptions, we can now calculate a new probability for a single dispersal event. The probability of X unsuccessful trials before a success on the $X + 1$th trial is:

$$p(x+1)q_1q_2,\dots q_x \quad x = 0, 1, 2, \dots \tag{2}$$

where $q_i = 1 - p_i$ (the probability of no dispersal in trial i). For most cases the value of q_i is very close to 1. By plotting the probability of X failures before the $X + 1$th trial, against various values of x (time), it is clear that the probability of dispersal on the $X + 1$th trial is very small indeed (Fig. 2). This geometrical model, one of a series of possible models, indicates that the probability of crossing the water from Africa to Madagascar is virtually zero.

Because dispersal is an extreme event, one should explore the analyses further using the theory of extreme events. This is beyond the scope of this paper, which is merely to illustrate that Simpson's sweepstake model is not a good explanation for the colonization of Madagascar by non-volant mammals.

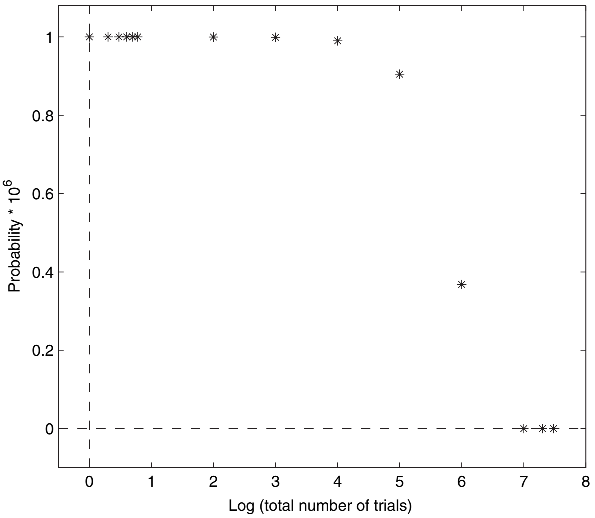

Figure 2 Graph showing probability of X failures before success on trial (time) $X + 1$. The starting probability of successful dispersal is taken from Simpson's (1952) probability of $p_i = p = 1/10^6$, for all i. The probability of dispersal on the $X + 1$th trial is very small. Note that the time scale (x-axis) is given on a log scale, ranging from 1 to 30 million trials.

Modelling the fate of a natural raft emerging from an estuary on the East African coast

A floating island raft with no ocean currents

Let us consider a floating island drifting down a river, supporting a group of lemurs (Fig. 3). First, we consider the simplified scenario where there are no ocean currents, and once the raft enters the ocean through the river mouth with velocity v, drag is the only force acting on the raft. It might be obvious that under these conditions the raft will not move far, but a detailed analysis of this scenario is necessary, as it forms our null hypothesis. The drag force is directed in the direction opposite to that of the vessel's motion, so the raft will experience a deceleration. The acceleration is given by Newton's second law:

$$a = \frac{F_\mathrm{d}}{m} \tag{3}$$

where m is the mass of the raft (and the lemurs), and F_d the force given by the Drag Equation:

$$F_\mathrm{d} = \frac{C_\mathrm{d}\rho A v^2}{2}. \tag{4}$$

In this equation the following parameters contribute to the force: C_d is the dimensionless drag coefficient that describes the raft's aerodynamic properties, ρ is the density of the fluid, A is the surface area of the projection of the raft onto a plane perpendicular to the direction of motion and v is the velocity of the raft with respect to the fluid.

If C_d, ρ and A are constant, the force can be expressed as being proportional to the square of the velocity:

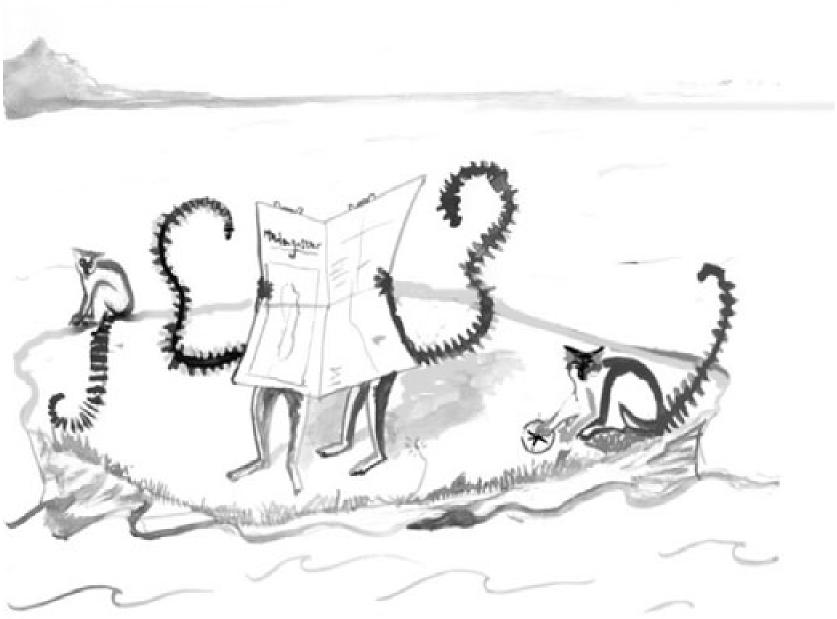

Figure 3 Our diagram showing lemurs navigating a floating island raft in an attempt to colonize Madagascar.

$$F_d = C'v^2 \tag{5}$$

where

$$C' = \frac{C_d \rho A}{2}. \tag{5a}$$

Assuming that the mass of the raft remains constant, combining equations 3 and 5 gives:

$$a = Cv^2 \tag{6}$$

where

$$C = \frac{C'}{m} = \frac{C_d \rho A}{2m}. \tag{6a}$$

Thus, if surface area and mass remain constant, as the velocity decreases due to drag, the drag will decrease. To obtain the velocity and position of the raft as a function of time (t), we require a differential equation, which yields the following expressions:

$$v(t) = \frac{1}{Ct + (1/v_0)} \tag{7}$$

and

$$s(t) = \frac{\log(Ctv_0 + 1)}{C}. \tag{8}$$

There are two constants in these expressions: C, which contains information about the raft and the fluid it floats through, and v_0, the raft's original velocity (remembering that at this stage the fluid is assumed to be free of currents). It is necessary to obtain estimates for the constants. SI units will be used throughout, including time in seconds. The density of water is 1000 kg m^{-3} (the value would be slightly higher for salt water, but this value is an order estimate calculation). Let us consider a rectangular raft 10 m long, 10 m wide and 5 m high. If the raft's density is 800 kg m^{-3}, 4 m will be submerged with 1 m above the water. The air drag on that 1 m can be ignored here. The surface area A is then 40 m^2, and the raft's mass, m, 400,000 kg (the mass of the water displaced). The mass of the lemurs can also be ignored. The drag coefficient, C_d, is usually determined experimentally for specific objects. Sample values can be found on the Engineering Toolbox website (http://www.engineeringtoolbox.com). Typical values are between 0.2 and 2, with a cube having a value of 0.8, so assigning our raft a value of 0.5 cannot be far out. Combining these gives $C = 0.025$. Table 1 shows the raft's speed and the total distance it will have travelled after 1 min, 1 h, 1 day, 1 week and 1 month for different initial velocities exiting the river mouth.

From Table 1 it is clear that, in the absence of ocean currents or other tumultuous events, the lemurs would not reach Madagascar (*c*. 430 km from Africa) by a floating island raft before running out of food or dying from exposure. Importantly, the velocity of the raft as it enters the ocean appears to be of little relevance, as it only affects the distance travelled in the first minutes of the journey. Even if the raft had the design of a supersonic fighter jet ($C_d = 0.016$), and entered the ocean at Mach 2 (700 m s^{-1}), after 1 h the speed would be reduced to 0.35 m s^{-1}. The raft would cover less than 10 km in that time. During the next year, it would cover another 11 km, still well short of Madagascar. As stated earlier, these conclusions might have been expected. However, we have not only proved conclusively that the null hypothesis cannot be valid, but shown that, for the more realistic models including currents and winds, the initial velocity of the raft can always be ignored.

A floating island raft in the presence of ocean currents

Based on the results for a perfectly still ocean, we can assume that the shape of the raft, as well as its velocity upon entering

Table 1 Velocities of a floating island raft and distances travelled in the absence of ocean currents, calculated from equations 7 and 8

	$v_0 = 1$ m s^{-1}	$v_0 = 10$ m s^{-1}	$v_0 = 100$ m s^{-1}
v after 1 min	0.40 m s^{-1}	0.62 m s^{-1}	0.66 m s^{-1}
s after 1 min	37 m	110 m	200 m
v after 1 h	0.01 m s^{-1}	0.01 m s^{-1}	0.01 m s^{-1}
s after 1 h	180 m	270 m	360 m
v after 1 day	4.6×10^{-4} m s^{-1}	4.6×10^{-4} m s^{-1}	4.6×10^{-4} m s^{-1}
s after 1 day	310 m	400 m	490 m
v after 1 week	6.6×10^{-5} m s^{-1}	6.6×10^{-5} m s^{-1}	6.6×10^{-5} m s^{-1}
s after 1 week	380 m	480 m	570 m
v after 1 month	1.5×10^{-5} m s^{-1}	1.5×10^{-5} m s^{-1}	1.5×10^{-5} m s^{-1}
s after 1 month	440 m	540 m	630 m

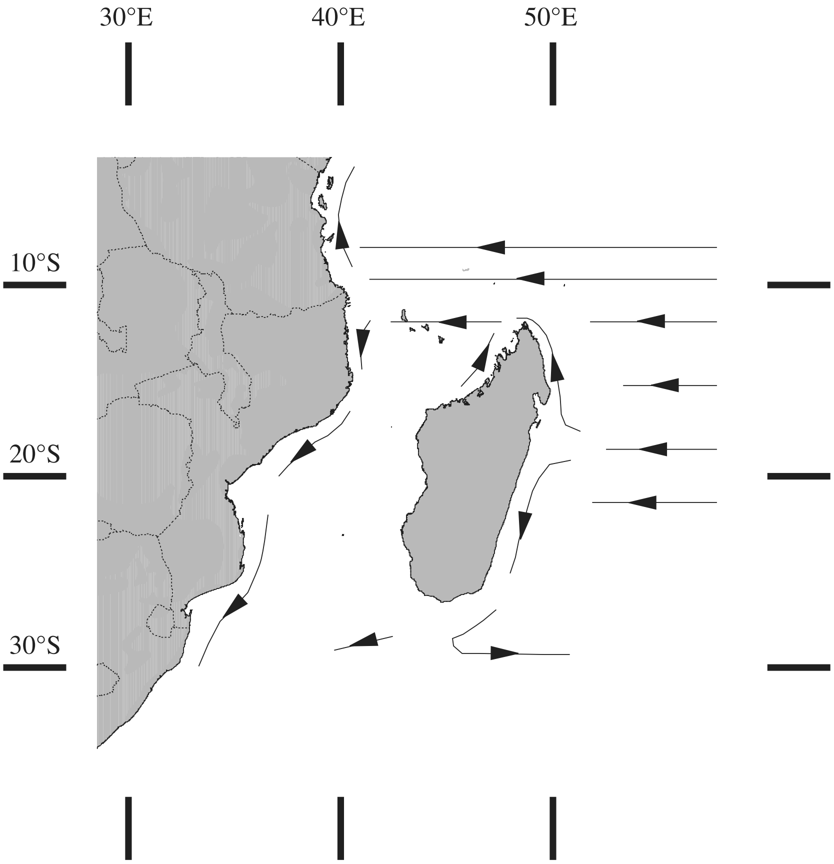

Figure 4 Surface ocean currents around Madagascar and the south-eastern coast of Africa, based on Figs 1 and 6 of Lutjeharms *et al.* (2000).

the ocean, are not factors that would influence its trajectory. In the presence of ocean currents the equations remain similar. Recall that v, the velocity of the raft, is defined with respect to the fluid. Ocean currents in the south-eastern Indian Ocean have speeds ranging from 0.1 to 2.0 m s^{-1} (e.g. Lutjeharms *et al.*, 2000). From Table 1 we can see that after 1 h the raft's velocity would be at the most 10% of the speed of the current, and by then the raft would have travelled a few hundred metres. We can thus assume that for any intercontinental journeys the direction and speed of the raft are virtually identical to those of the ocean currents.

At this point it is necessary to discuss the nature of the ocean currents around Madagascar and off the east coast of Africa. Figure 4 is based on the data of Lutjeharms *et al.* (2000). The South Equatorial Current flows westwards between 8° S and 22° S until it reaches the east coast of Madagascar (Woodberry *et al.*, 1989) when the flow splits, with the northern branch rejoining the South Equatorial Current. This current continues westwards until it reaches the African continent around northern Mozambique and southern Tanzania. There it divides again into two branches. The northern branch (the East African Coastal Current) does not concern us here, while the southern element originates the Mozambique Current, which follows the African coast and on reaching South Africa becomes known as the Agulhas Current.

The southern branch of the South Equatorial Current, known as the East Madagascar Current, follows the east coastline of Madagascar from 18° S (Hastenrath & Greischar,

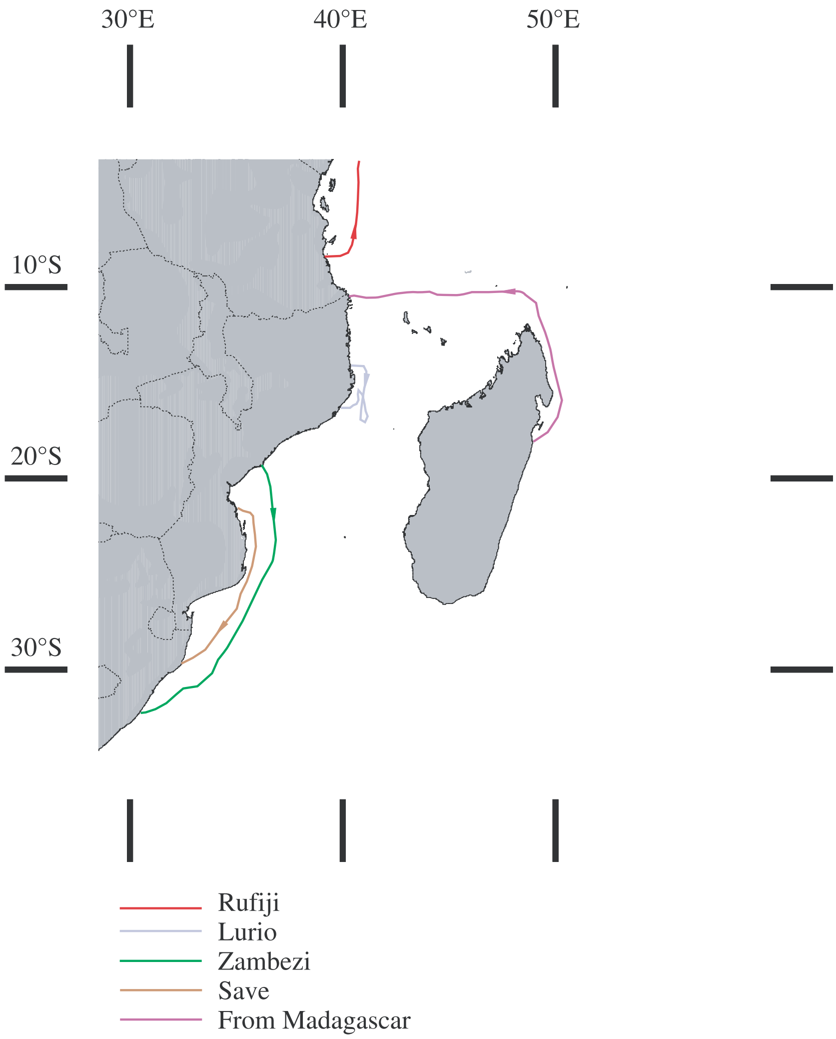

Figure 5 Trajectories of journeys from the mouths of rivers discussed in the text.

1991). It does not join the Mozambique–Agulhas Current, but retroflects back to the east at 27° S (Lutjeharms *et al.*, 1981). However, Lutjeharms *et al.* (2000) state that small, intermittent contributions to the Agulhas Current from the East Madagascar Current can occur by way of current rings.

The Mozambique Current is the most prominent feature of the Mozambique Channel between Madagascar and the African coast, and dominates the flow for 100–200 km off the African coast. This current is usually strong (over 1 m s^{-1} in places), though not consistently so. In places it appears virtually non-existent (e.g. at 20° S), while at 15° S a slight north-flowing current is observed. On the Madagascar side of the Mozambique Channel the currents are very weak (*c.* 0.1 m s^{-1}). Most of the drift is directed north and north-east, to join the strong South Equatorial Current flowing westwards from over the northern tip of Madagascar.

So what would happen to a floating island raft washed down an African river? If the raft gets caught in a coastal current it will follow it until it escapes the current. Escape could occur as a result of random motions (due to wind or swells) perpendicular to the current direction. Recall that, irrespective of its initial velocity, the raft will only be about 100 m from shore, while the coastal currents are typically over 100 km wide. It thus seems fair to assume that the only way the raft will escape the current is by being beached back on the African coast (see Fig. 5).

If the river in question was the Rufiji, which until *c.* 40 Ma might have been the outlet of the major river draining the Congo Basin (Stankiewicz & de Wit, in press), the raft would follow the African coast north given that its outlet is at a latitude of 8° S (i.e. north of the South Equatorial Current). Alternatively, exiting from the Lurio River (14° S), the raft would drift with the Mozambique Current but would not get past 15° S, where the drift is directed north. The raft might oscillate south and north for a while, before eventually being beached not far from the outlet of the Lurio (Fig. 5). Finally, emerging from the mouth of the Zambezi (18° S) or the Save (21° S), the raft would follow the African coast south, and, provided it remained afloat long enough, would land its lemur crew somewhere in southern Mozambique or KwaZulu-Natal.

By contrast, interesting scenarios transpire if we consider a raft leaving Madagascar. If the departure point occurred from the northern part of the island (either on the west or the east side), the raft would flow north until 12° S, where it would be picked up by the South Equatorial Current and perhaps deposited on the African coast at that latitude. This journey of *c.* 600 km, assuming a current speed of 0.7 m s^{-1}, would take 10 days. If the raft left the east coast of Madagascar south of the 18° S parallel, it would follow the coast south, and provided it remained afloat and did not beach back on land it might follow the current once it retroflects back east. As some of the waters from that current are believed to reach the Agulhas Current, so might the lemurs.

In detail, ocean current flow in the Mozambique Channel is not as straightforward. For example, Harris (1972) proposed that the channel is dominated by three large anticlockwise circular eddies. There has been much subsequent debate regarding this circular flow. Such a pattern of circulation raises the possibility of a raft reaching Madagascar in a southern arc after entering the channel from mainland Africa. However, the eddies have a diameter of less than half of the channel's width, and tend to stay in the centre of the channel. Schouten *et al.* (2002) demonstrated the path of a drifter released in the middle of the narrowest section of the channel. The drifter was observed to complete 10 loops of no more than 150 km in diameter, while continually moving south-west. After 2 months it exited the channel and stopped circling. The authors suggested that these eddies have their origin in west-flowing Rossby waves near the Comores. Chapman *et al.* (2003) have shown that eddies are not initiated north of the Comores, increasing the probability that the islands are responsible for the circular flow pattern. If that is the case, the lemurs could not have benefited from such eddies, as the Comores were formed at less than 10 Ma (Melluso & Morra, 2000; de Wit, 2003). Even if circular eddies were present in the channel at the time the lemur ancestor is assumed to have embarked on its journey, the eddies do not come sufficiently close to either coast to capture a coastal raft. It is worth repeating that the west-flowing currents north and south of the channel make the westwards journey infinitely more likely; i.e. even if an unusually large eddy carried inhabited flotsam to Madagascar, one should expect some of the pioneers' descendants to make the return journey.

A floating island raft with a tree acting as a sail

This scenario consists of a raft similar to the one in the previous example, but with a tree growing on the lawn and acting as a sail. In this case the wind speeds over the eastern Indian Ocean become relevant. The force on the raft is then the sum of two forces resulting from two drag equations: the ocean current drag on the submerged section of the raft and the wind drag on the tree above the water level. The parameters for the currents can be assumed to be the same as in the previous example. In the wind drag equation, the air density value of 1.25 kg m^{-3} was used. The drag coefficient can be assumed to be the same as that of the rest of the raft (0.5), while the surface area of a tree 10 m high and 3 m wide, combined with the 10 m^2 of the raft above water, gives $A = 40$ m^2, the same as the A in the current drag equation.

In this problem it is therefore necessary to include the regional surface ocean currents as well as the surface wind speeds. The currents used were those shown in Fig. 4. The winds were taken from Hastenrath & Greischar (1991). For most of the year the surface winds in the Mozambique Channel blow north-westwards. In January, however, this direction is reversed. As this is the only scenario that would aid the raft's journey, it is the only one considered here. The wind speeds reported by Hastenrath & Greischar (1991) range from 2 to 4 m s^{-1}. Off the coast of Tanzania the wind direction is mostly south, becoming south by south-east as one approaches the northern part of Madagascar. Further south, the pattern becomes somewhat more complicated. Figure 6 shows the wind direction in the area, based on Fig. 2a of Hastenrath & Greischar (1991).

It should be noted that in the southern section of the channel the winds within 100 km of the African coast blow west – this direction would only inhibit the progress of a raft from the outlet of either the Zambezi or the Save. Similarly, a raft leaving the Rufiji Delta would rapidly be pushed back onto the mainland. The only place from which the wind might help the raft cross the Mozambique Channel is the outlet of the Lurio. Even then, the raft might be guided by the winds blowing south-west, and be taken back to Mozambique. However, let us assume the most favourable scenario, namely a steady wind blowing at 5 m s^{-1} over the entire Channel. With the addition of wind drag, the differential equation governing the motion of the raft becomes intractable, so a computer program was written to simulate the flow, given the raft's initial position and regional currents and winds. Figure 7 shows the trajectory of the raft 1 week after exiting from the mouth of the Lurio, given the currents in Fig. 4 and a 5 m s^{-1} wind blowing south-east. Simons (1976, p. 51) has estimated that lack of food and water, salt imbalance and environmental stresses due to exposure 'would render most small primates comatose or unconscious in 4–6 days', indicating that this rate of progress would be far too slow for a successful colonization event. The duration of the channel crossing from the mouth of the Lurio could be reduced to only 10 days if the raft was subjected to a continuous wind of 20 m s^{-1}. This velocity corresponds to Beaufort force 10, at which trees growing on steady ground are uprooted. A tree acting as a sail for a lemur family crossing the ocean is likely to break much earlier. Additionally, such weather conditions are unlikely to increase the estimated survival period of less than 1 week; if anything, they are likely to reduce it.

A tornado transporting animals

There are countless accounts of objects, animals and even people being picked up by tornadoes and deposited some distance away. A statistical analysis of these incidents is very difficult, as only identifiable objects can be included. If a rock is transported by a tornado it is unlikely that its exact place of

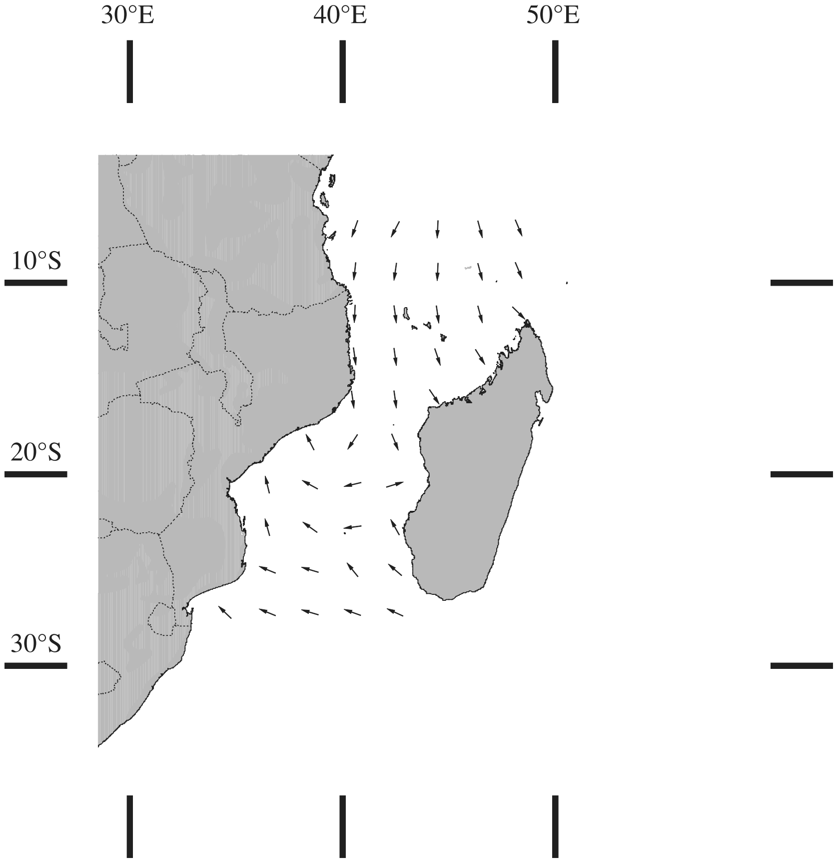

Figure 6 Surface wind directions in the Mozambique Channel, based on Fig. 2a of Hastenrath & Greischar (1991).

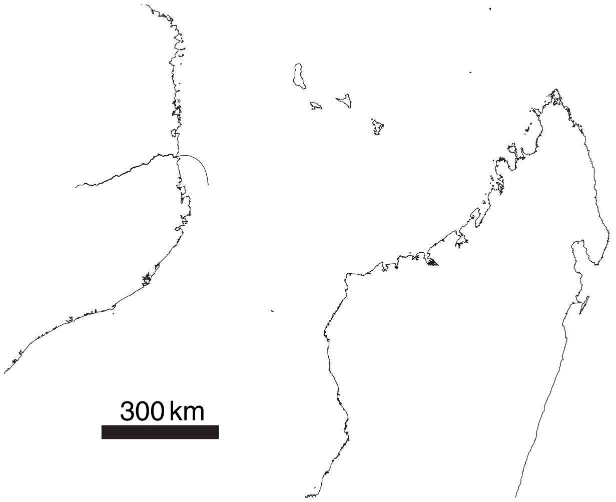

Figure 7 Trajectory of a raft with a tree acting as a sail 1 week after exiting from the mouth of the Lurio River. Currents as Fig. 4, wind assumed constant 5 m s^{-1} blowing south-east.

origin can be determined. Objects that can be traced to their place of origin include photographs, restaurant menus or even a wedding dress (O'Toole, 1993). Transport of objects over many kilometres is not unheard of: the largest distance travelled by an identifiable object is around 300 km. The longest distance covered by an object weighing 1 lb (*c.* 0.5 kg) or more is just over 150 km (a bag of flour). Could a 0.5 kg (pregnant) lemur be carried 430 km to Madagascar, and, if so, could it (and its foetus) survive the journey, to say nothing of the landing? Another question worth investigating, is whether tornadoes stronger than any observed so far in the modern era have occurred in the past, and just what velocities tornado wind speeds can reach?

The scale commonly used for classifying tornadoes by their intensity is the *F*-scale (after Fujita, 1981). The scale covers the range from the top of the Beaufort scale (*c.* 18 m s^{-1}) to the speed of sound (*c.* 330 m s^{-1}), dividing it into 12 intervals. The *F*-scale value is defined as:

$$F = \left(\frac{v}{6.3}\right)^{2/3} - 2 \qquad (9)$$

where v is the wind velocity in m s^{-1}, the resulting value of F being rounded down to the nearest integer. Thus F can take on a value from 0 to 11, and tornadoes of a particular intensity are referred to as *F*0, *F*1, etc. No tornado has ever been classified higher than *F*5. The minimum speed for an *F*6 tornado is 143 m s^{-1} (513 km h^{-1}), and the fastest recorded wind speed is 509 km h^{-1} in the Oklahoma tornado of May 1999 (http://news.bbc.co.uk/1/hi/sci/tech/342507.stm). Table 2 shows the wind speeds corresponding to observed intensities, a description of such an event and the percentage of observed tornadoes that fall into that intensity class. The last statistic comes from Geerts (1999), who compiled tornado records in the

Table 2 Statistics of observed tornadoes in the US (data from Geerts, 1999)

	Wind velocity			
Fujita scale	v (m s^{-1})	v (km h^{-1})	Description	% of tornadoes
*F*0	18–33	64–118	Gale tornado	83
*F*1	33–50	118–181	Moderate tornado	11
*F*2	50–70	181–254	Significant tornado	4
*F*3	70–93	254–333	Severe tornado	1.8
*F*4	93–117	333–420	Devastating tornado	0.9
*F*5	117–143	420–513	Incredible tornado	0.4

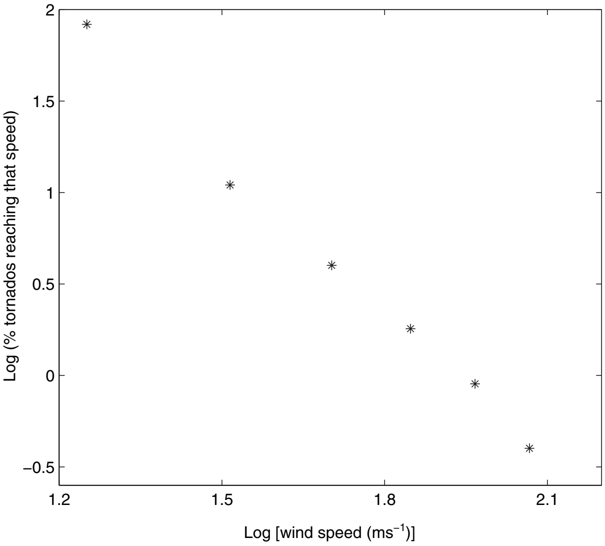

Figure 8 Logarithmic plot of tornado frequency as a function of their magnitudes using data in Table 2, taken from Geerts (1999).

USA. Figure 8 shows a logarithmic plot of the frequency of tornadoes of a particular intensity as a function of the minimum wind speed for that intensity. The inverse linear regression is excellent, with a correlation coefficient of 99.7%. It could thus be inferred that the occurrence of tornadoes follows a power-law distribution over the observed range. If this distribution extrapolates to higher wind speeds, expected numbers of higher-intensity tornadoes can be estimated by extending the regression line. At least 1000 tornadoes are recorded in the USA every year (National Severe Storms Laboratory survey). Using the statistics of Geerts (1999), just 4 out of every 1000 tornadoes are expected to be of intensity *F*5. Extending the regression in Fig. 8 linearly yields an expected value of approximately 2.5 *F*6 tornadoes, about 1 *F*9, and 0.35 *F*11 tornadoes. Thus, on that basis, in the USA alone we might expect that there would be two or three *F*6 tornadoes a year, and a tornado with winds approaching the speed of sound every 3 years! These prodigious tornadoes would be unlikely to go unnoticed, and their absence from observations over the existing record leads to the conclusion that the distribution does not extend past *F*5 tornadoes. The upper limit of that range, or perhaps the lower limit of the *F*6 range, thus constitutes the maximum possible wind speed. If higher speeds were possible, they would have been observed by now. This view accords with the appearance in Fig. 8 of curvature downwards at the higher wind speeds.

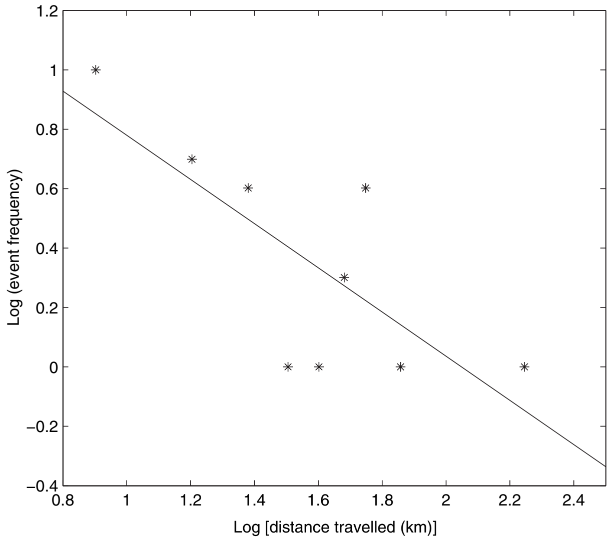

Figure 9 Logarithmic plot of the observed frequency of objects of mass greater than 0.5 kg travelling a specified distance after being lifted by a tornado as a function of that distance. Data from Snow *et al.* (1995).

Unless tornadoes were stronger in the past, the probability of objects being carried long distances must have been the same as today. One of the very few analyses of this ‘debris fallout’ is provided by Snow *et al.* (1995), who assembled data from over 12,000 tornadoes since 1871. In all, they encountered 29 reports of an object weighing more than 1 lb (*c.* 0.5 kg) being carried more than 5 miles (*c.* 8 km). Nineteen of these travelled less than 20 miles (*c.* 32 km). No object weighing more than 0.5 kg has been observed to travel half of the minimum distance between Madagascar and Africa. The frequency of travelling a particular distance as a function of that distance is shown in Fig. 9. The correlation of the logarithmic plot is 79.6%; given only 29 data points, this plot suggests a power-law distribution. If the regression is extrapolated to a distance of 400 km, the corresponding percentage frequency of an object being transported that distance is estimated at 0.39. Thus, assuming this is a valid extrapolation, one needs to study over 30,000 tornadoes to expect one recognizable object weighing more than 0.5 kg to be transported at least 400 km.

The use of tornado data for inferences about cyclone effects is likely to be exaggerative. But, playing lemur’s advocate, suppose we allow such wind speeds to be attained within cyclonic phenomena. The number of cyclones around Madagascar is about 10 per season (November–April). Of these cyclones, most stay east of the island: in the past five seasons there have been only 10 cyclones in the Mozambique Channel (Fig. 10). The principal direction of their movement is westwards, but some, like Fari, turn back east over the channel. None of these,

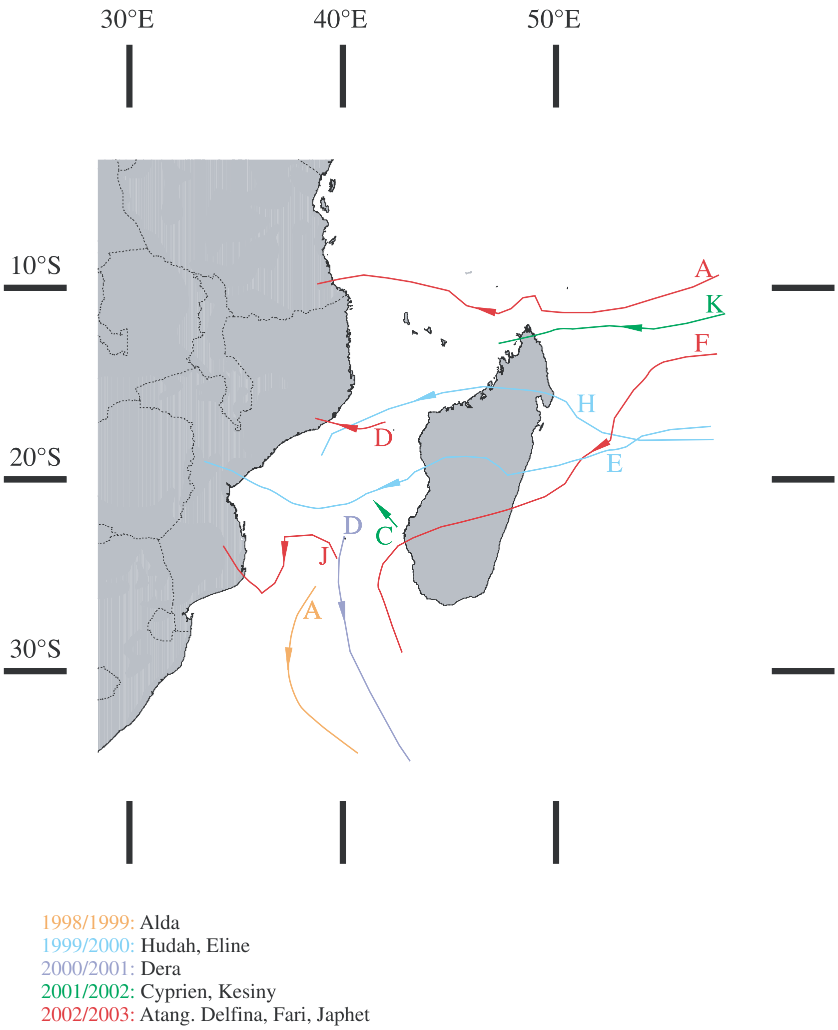

Figure 10 Tropical cyclones over the Mozambique Channel in the seasons 1998/99 to 2002/03. Data from the UK Met Office (http://www.metoffice.com/).

however, turns over Africa and returns to Madagascar. If one did that every season, every 30,000 years an object weighing 0.5 kg or more might be hurled from Mozambique to Madagascar. Awaiting the transport of a 3 kg object will obviously need a more extensive period of time, and the probability of this 3 kg object being a lemur is correspondingly smaller. Then there is the problem of a creature surviving such a ride. Professor John Snow commented in his personal communication that 'One negative on lofting and transporting larger living entities: the core region of a tornado is most likely a very harsh environment due to flying debris and detritus. Living through it would be a great challenge for anything of any size.' When one considers that a male and female are needed to land safely and intact, within a few kilometres of each other, in the same event or at most a few years apart, the probability becomes ludicrously small. The odds are not much better for a pregnant female, who would then need to breed with her offspring in order to found a new population.

DISCUSSION

It is not our contention that sweepstakes dispersal can never take place, under any conditions or involving any groups of organisms. On the contrary, there is concrete evidence for colonization of islands by rafting vertebrates, and these studies are highly pertinent to this investigation for the boundaries they set regarding the conditions under which dispersal can occur. Censky *et al.* (1998) made observations of over-water dispersal of green iguanas between islands in the Caribbean. The lizards arrived on the islands of Barbuda and Anguilla on extensive mats of logs and uprooted trees, although the authors were of the opinion that they had originated on Guadeloupe. Figure 11 shows the relative positions of the islands, as well as the directions of the surface ocean currents and the path of hurricane Luis, which passed through the archipelago on 4 and 5 September 1995, travelling in a north-westerly direction and uprooting trees and other vegetation. On 22 September, the first iguanas were sighted on Barbuda, 150 km from Guadeloupe. They had covered the 270 km journey to Anguilla by 4 October. It was shown earlier in this paper that flotsam velocity would stabilize at the value corresponding to the surface current velocity within a matter of hours. The surface current speeds in this area of the Caribbean are of the order of 10–12 cm s^{-1} in autumn (Arnault, 1987). This corresponds to 8.6–10.4 km day^{-1}. If the speed of the raft is indeed determined by the speed of the

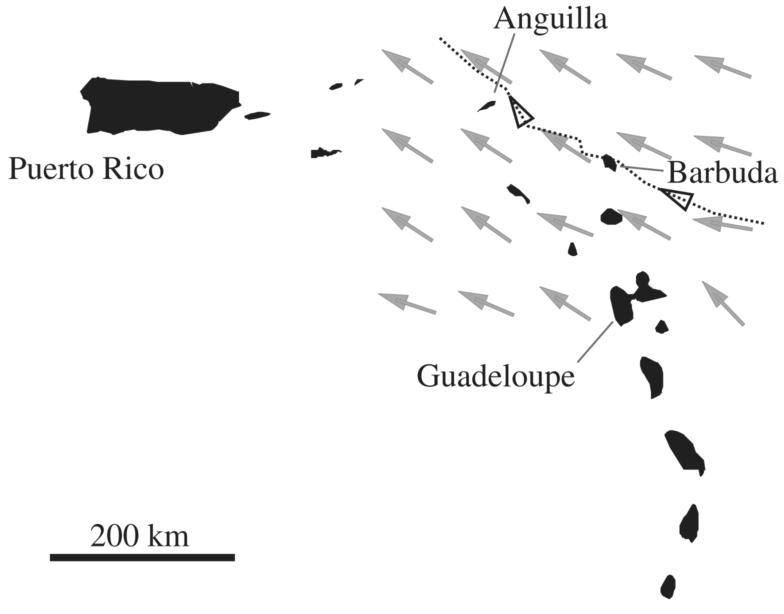

Figure 11 Section of the Caribbean archipelago in which colonization of islands by rafting vertebrates occurred. Green iguanas, apparently deriving from Guadeloupe, arrived on the islands of Barbuda and Anguilla on mats of vegetation (Censky *et al.*, 1998). Black = islands; grey arrows indicate the surface ocean currents (after Arnault, 1987); the dashed line marks the path of hurricane Luis, which passed through the region on 4 and 5 September 1995. See text for further explanation.

surface current, we would predict that the 150 km journey from Guadeloupe to Barbuda would take between 14 and 17 days (iguanas were sighted 16–17 days after the hurricane), and the 270 km journey from Guadeloupe to Anguilla would take between 26 and 30 days (iguanas beached 29–30 days after the hurricane). Thus, if Guadeloupe was indeed the source of itinerant lizards, the currents took them directly to the two islands at a speed corresponding exactly to current velocities.

Similarly, *Anolis* lizards have recolonized islands in the Bahamas up to 300 km away after the islands were denuded by hurricanes (Calsbeek & Smith, 2003). The authors managed to discount immigration as a result of direct transport by the hurricane; rather, immigration occurred by rafting, travelling an average distance of 124 km in approximately 1 week with a surface current of 20 cm s^{-1}. *Anolis* lizards are capable of surviving long-term exposure to sea water, and in fact swim in the ocean. The authors demonstrated that gene flow between the islands is determined by winds and ocean currents.

Returning to the focus of our study, the Afrotropical region, phylogenetic studies of other squamates, including gekkonid lizards (Kluge & Nussbaum, 1995) and chameleons (Raxworthy *et al.*, 2002; Rieppel, 2002), have implicated over-water dispersal as essential for explaining their biogeography. In both of these cases dispersal events have been in the direction of winds and ocean currents, i.e. from Madagascar to Africa.

Thus, with favourable currents and wind speeds, dispersal over water is indeed possible. However, in defiance of current and wind directions, the probabilities of successful dispersal are so small that even vast tracts of time cannot compensate. Perhaps the question that we should be asking about lemuroid dispersal is why there has not been a colonization event from Madagascar to the African mainland, given that the currents and cyclone paths would favour dispersal in this, and not the other, direction.

The other aspect of these studies that requires comment is that all of these successful sweepstakes events have involved reptiles, which do not face the energy demands of maintaining a constant body temperature that mammals do. Some authors have suggested the over-water dispersal of lemurs, tenrecs and rodents to Madagascar was facilitated by their ability to lower their energy demands by going into a state of torpor or hibernation (Martin, 1972; Yoder, 1996; Kappeler, 2000; Yoder *et al.*, 2003). The likelihood of the waif lemur using hypometabolism in this way has been investigated by J. C. Masters *et al.* (unpublished data), who estimated the body size of the ancestral lemur both from the fossil record and by using independent phylogenetic contrasts. According to their reconstruction, the ancestral lemur is likely to have weighed approximately 2 kg, which is well outside the body size range that defines the use of hypometabolism in mammals today. Additionally, the galagos – mainland relatives of the lemurs that shared a common ancestor with them around 60 Ma – are not known to use torpor or hibernation, even in stressful environments (Mzilikazi *et al.*, 2004).

Krause *et al.* (1997) have suggested that crossings of the Mozambique Channel by rafting may have been somewhat easier in the Late Cretaceous (*c.* 65 Ma) to Late Eocene (*c.* 40 Ma), since Madagascar lay *c.* 15° farther south than it does now, and the prevailing winds and currents may have been more conducive to dispersal. On the other hand, as Madagascar moved north on the African Plate during the Palaeocene–Eocene, across 30° S latitude, most of the island would have passed through the subtropical arid zone and this is unlikely to have generated an environment hospitable to arboreal primates (Wells, 2003). However, very little is known about Madagascar's Cenozoic climatic history (and therefore adjacent ocean currents and wind directions) because of the lack of preserved continental deposits and fossils (Wells, 2003; de Wit, 2003). Modern Indian Ocean circulation dates back to the Late Eocene (*c.* 40 Ma), and available regional palaeoclimatic data suggest a relatively stable climate regime for Madagascar since that time (Wells, 2003).

Prior to the Palaeocene, the general oceanic circulation of the Indian Ocean, and hence around Madagascar, must have been distinctly different because of the central position of India in the proto-Indian Ocean at that time (Reeves & de Wit, 2000; Wells, 2003; de Wit, 2003). In addition, because of the more southerly position of Madagascar–Africa, north-westerly prevailing winds would have dominated across the proto-Mozambique Channel (Wells, 2003). To what degree this may have facilitated migration from Africa to Madagascar remains to be analysed, but the calculations presented in this paper suggest that the probability of successful colonization at that time by wind-aided rafting across this distance is unlikely. Thus, either episodic emergence of inter-channel islands along the Davie Fracture Zone during the end of the Mesozoic and early Cenozoic played a significant role in facilitating this colonization process (Leclaire *et al.*, 1989; Krause *et al.*, 1997; McCall, 1997; de Wit, 2003) or other, more cryptic, processes were involved. Alternatively, perhaps Africa was not the source of all of the Malagasy mammals, including the lemurs (see e.g. Martin, 2003). We need to seek another characteristic that is shared by pseudo-aardvarks, tenrecs, carnivores and primates that led to their colonization of Madagascar other than the fact that they are all subject to freak climatic events.

In conclusion, our calculations show that, with our current state of knowledge of statistics, geophysics, hydrodynamics and lemur biology, sweepstake tickets between Africa and Madagascar were simply not for sale.

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