**Geography 144 Midterm**
**Dahl Winters**
**3/1/06**

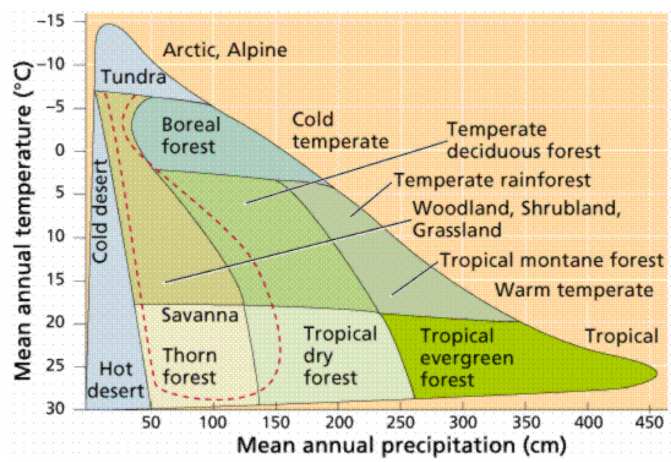
**1.** The physical dynamics of the ocean environment influences the distribution of terrestrial life by influencing 1) ocean-atmosphere heat transfer as well as precipitation, 2) the dispersal of terrestrial species to oceanic islands, 3) availability of marine food for terrestrial predators, and 4) the formation of coastal fog. The first two occur on global scales, while the last two act at landscape scales and larger (one to hundreds of kilometers).

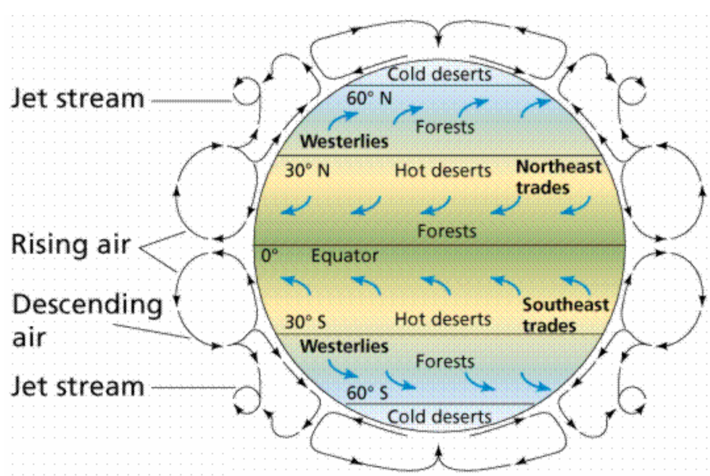
1) Influence on ocean-atmosphere heat transfer and precipitation

A major feature of the Earth's oceans is its currents, which are driven by surface winds resulting from solar heating of the atmosphere (Lomolino et al 2006). This circulation transports enormous quantities of heat from the Equator to the poles; without it, the higher latitudes would be even colder and the equatorial latitudes warmer than at present, leading to a shrinking of the extent of life in both the N and S hemispheres. It is because of the Gulf Stream's heat transport from equatorial areas to the north that London is warmer in winter than Toronto, even though it is closer to the North Pole.

Ocean currents also result in more moderate climates along coastal regions, since it takes a long time to transfer or remove significant amounts of heat from large bodies of water. Atmospheric temperature extremes are moderated in coastal areas so that they experience only small diurnal temperature variations compared to mid-continent areas, which are farther from the moderating influence of the oceans. Thus, the terrestrial species distributed along the coast will largely consist of species less tolerant of temperature extremes than those found in mid-continental areas.

The oceans are the primary source of evaporation, and is thus the primary source of precipitation. This is important to the distribution of terrestrial life because, as covered in class, all biomes of the world fall somewhere along a graph of temperature and precipitation (*right, top*). Ocean evaporation occurs at different rates depending on latitude because solar heating is more direct at the equator than at the poles, and the warmer equatorial air can hold more water than cold polar air. Global wind patterns, also driven by the differential solar heating (as well as the Coriolis force), determine where this water will rain back down (*right, bottom*). The distribution of precipitation has a great effect on the distribution of plants adapted to different levels of precipitation, as well




**Top and bottom: from Purves et al., Life: The Science of Biology, 4th Edition, by Sinauer Associates.**

as the animals that depend on those plants for food and habitat. These major wind patterns, which are the trade winds, westerlies, and polar easterlies, lead to the formation of world's major desert biomes over stable high-pressure zones where it seldom rains (Lomolino et al 2006).

With decreasing latitude comes increasing temperature, and we see a transition from cold tundra and boreal forests to warmer temperate forests and hot tropical forests. With decreasing precipitation we see a transition from forests to grasslands to deserts. Grasslands and deserts are more likely to be found in dry mid-continental regions because of their distance from oceans. Polar regions are dry because cold air cannot hold as much moisture as warm air, and because of both low precipitation and temperatures, not many terrestrial organisms can survive there. Finally, where cool water meets with hot, dry land, Mediterranean-type ecosystems are often found, such as those in southwestern California and Australia, southern Europe, western South Africa, and Chile in western South America (Lomolino et al 2006).

<u>2) Ocean circulation is important for dispersal to oceanic islands.</u>

Ocean currents are important for the dispersal of terrestrial species from the mainland to oceanic islands. They also select for the kind of terrestrial life that will exist there. If oceanic islands are not colonized by plant seeds, insects, and birds arriving by air, the only other natural method of arrival is by water. Some plants have evolved floating seeds that allow them to be dispersed by water to distant islands, and have become ubiquitous over large groups of islands. Being able to disperse from one island to another via ocean currents helps keep populations from becoming reproductively isolated. Insects can hitch rides on floating debris or use them as stepping stones in their flight to get to islands. However, larger terrestrial animals rarely make it to islands because they cannot float, and often cannot swim the necessary distances.

<u>3) Consequences of coastal productivity for terrestrial life at landscape scales</u>

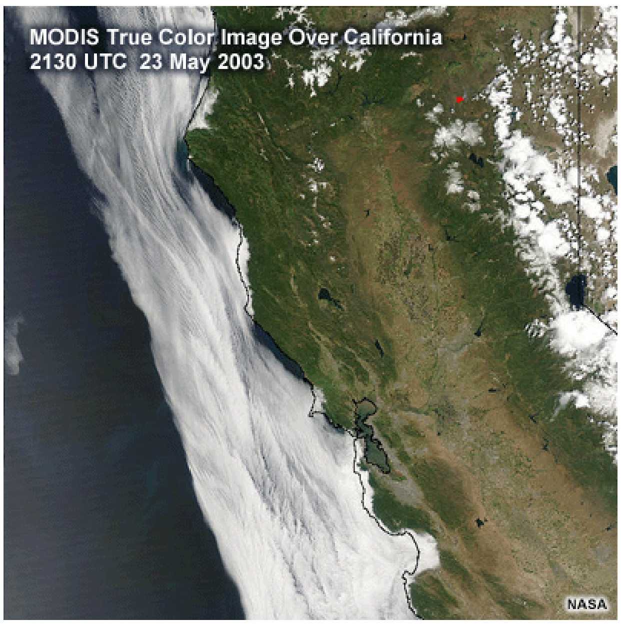
A map of global productivity shows us that ocean upwelling tends to occur along the west coasts of continents and at higher southern latitudes (Lomolino et al 2006). These zones, where cold, deep, nutrient-rich water comes up to the surface, are very productive areas for marine life because the increase in P and N boosts the growth of phytoplankton forming the base of the marine food web. An increase in marine life due to upwelling means increased abundance of terrestrial predators of marine species such as penguins, seals, and maritime birds which have evolved to take advantage of marine food opportunities. Thus, ocean dynamics is linked not only to the coastal distribution of these species, but also to their evolution as terrestrial predators in the marine food web.

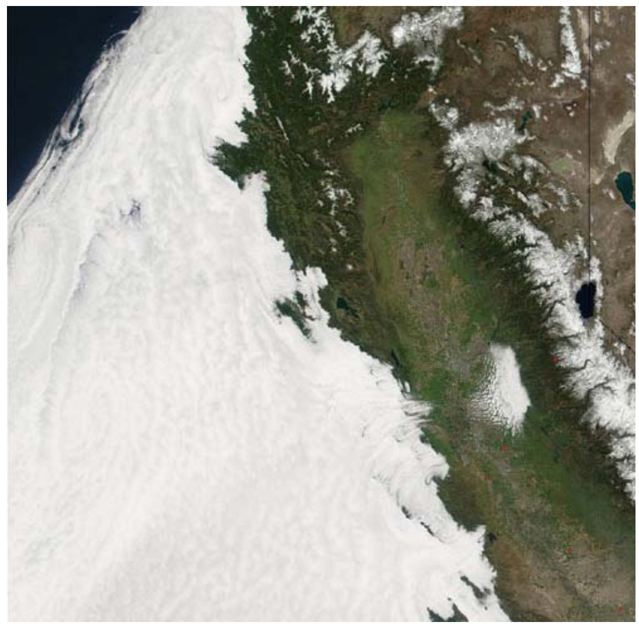
<u>4) Formation of coastal fog and coastal vegetation communities</u>

Coastal fog forms when warm, moist air from the land moves over cooler water, such as that brought to the surface by upwelling along the California coast. The warm, moist air cools and condenses to form fog, which drips into the soil and provides additional precipitation to plants in this otherwise dry region (Lundquist and Bourcy 2000). Thus, when fog forms, it creates an altitudinal moisture gradient on the western edge of coastal mountains that influences vegetation distribution at the landscape scale. The extra moisture allows wet-adapted species to thrive near sea level, while dry-adapted species typical of inland areas would be expected at higher elevations that receive less supplemental moisture from fog.

There is also a longitudinal gradient from the ocean and extending inland due to varying heights of fog formation, which are dependent on weather conditions such as sea surface temperature and the air temperature above land (Lundquist and Bourcy 2000). Fog height can vary between fog events as shown below for California, sometimes rising high enough to move halfway across the state. This means more available moisture for inland vegetation; a decline in fog events for whatever reason would exacerbate summer droughts in the area.

Fog events also have diurnal and longer-term temporal variabilities that affect the amount of moisture coastal plants can receive. Lundquist and Bourcy (2000) describe how coastal fog in CA and OR strongly follows a diurnal cycle, occurring mostly in the early morning along with lower surface temperatures and wind speeds, and very seldomly in the afternoon. In CA, fog events have also been correlated with the passing of a weak high pressure area over the state, and its dissipation by the movement of low pressure across the state. Thus, ocean conditions are strongly coupled with atmospheric conditions in determining where and when coastal fog will form, which in turn affects the distribution of terrestrial plant life.



**Left: 1 km resolution image showing fog extending up to and beyond the coastline in some places.**
http://meted.ucar.edu/mesoprim/dynfog/media/graphics/californiafog_1km.gif
**Right: image at roughly the same scale showing the fog at a height high enough to cover coastal mountains.**
http://www.geog.ucsb.edu/~joel/g110_w05/lecture_notes/california_fog/cal_coastal_fog1_sm.jpg

**2.** Islands have been such a major focus of biogeographic study not only because their isolation, simplicity, and abundance have aided our understanding of ecological principles, but also because of their unique assemblages of endemic species that are now the focus of conservation efforts.

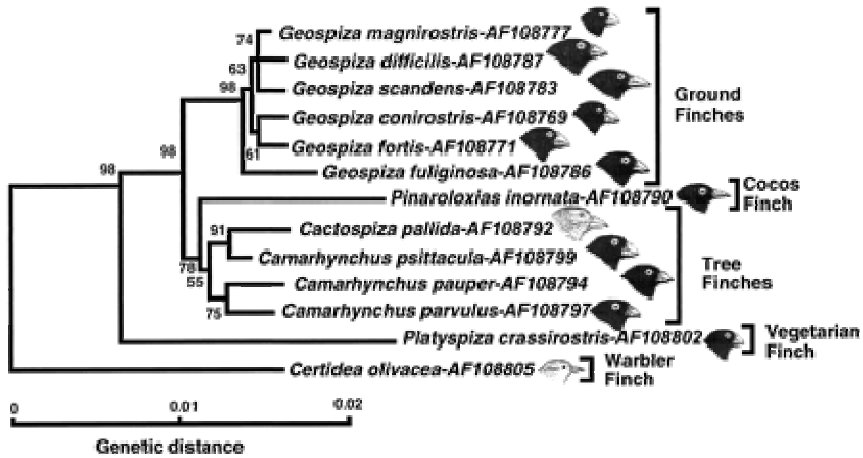
Islands are self-contained natural laboratories in which nature has already performed ancient experiments. Our textbook explains that islands are ideal subjects for natural experiments due to their being "well-defined, relatively simple, isolated, and numerous." Islands have obvious, strong boundaries that define areas within and beyond the island. They can vary in area, level of isolation, and presence of predators and competitors. This allows for an observational assessment of each of these abiotic and biotic factors on community structure, if we can select a group of islands where we can control for or minimize variation in all factors except those of our hypothesis. This selection is aided by the abundance of islands available, so that islands can be selected that are similar in climate, geology, or even biota.

Oceanic islands are not the only places where these natural laboratories can be found. Under the ocean, coral reefs and hydrothermal vents can serve as islands for species adapted to these environments. On land, lakes and streams are islands for aquatic organisms. For terrestrial organisms, islands can be mountaintops, caves, or serpentine soils. In all these places, we can observe how species have evolved in response to different sets of ecological factors.

The importance of islands to biogeography was well summarized by MacArthur and Wilson in their seminal book *The Theory of Island Biogeography*: "By their very multiplicity, and variations in shape, size, degree of isolation, and ecology, islands provide the necessary replications in natural 'experiments' by which revolutionary hypotheses can be tested" (MacArthur and Wilson 1967). Islands allow us to easily observe the results of experiments that nature had already set up thousands or millions of years ago, when the islands were created and populated. The colonizing species have had the time to evolve in response to the novel selective pressures they encountered. Novel abiotic selective pressures, such as a different soil type or moisture availability, and biotic ones such as the presence/absence of competition and the availability of unoccupied ecological niches, can act over great lengths of time to shape island communities.

Most islands are too big for us to perform our own experiments on them, but it is possible to find very small islands and successfully manipulate them in studies. In the classic study by Wilson and Simberloff (1969), seven mangrove islands in Florida Bay were covered and fumigated, effectively defaunating them and allowing the recolonization process to be studied. The only animals on the island were arthropods, there were only 20-40 species at any one time, and the islands were relatively small, making it feasible to identify and document every species on the island (Simberloff and Wilson 1970).

The simple ecologies of islands have aided the discovery of revolutionary ecological principles. These relatively small units of land, or water in the case of streams and lakes, have provided us with much simpler systems in which to study ecology compared to a continent or an ocean. Islands are often species-poor compared to the mainland due to their smaller area, which simplifies their ecology and has helped to make ecological principles easier to discover. Some of these principles include *island biogeography*, with its idea that the number of species on an island is the result of a dynamic equilibrium between immigration and extinction; the *species-area relationship*, which recognizes that island area directly affects that immigration and extinction; *metapopulation dynamics*, which is closely related to island biogeography and involves populations existing on habitat islands surrounded by an unsuitable matrix; *adaptive radiation*, which is the evolutionary divergence over time of a founder species to fill available ecological niches; and SLOSS (*single large or several small*), a continuing debate over whether to preserve a single large habitat island which will have more species less prone to extinction, or several small habitat patches, which will capture more habitat and genetic diversity but also be more prone to extinction.

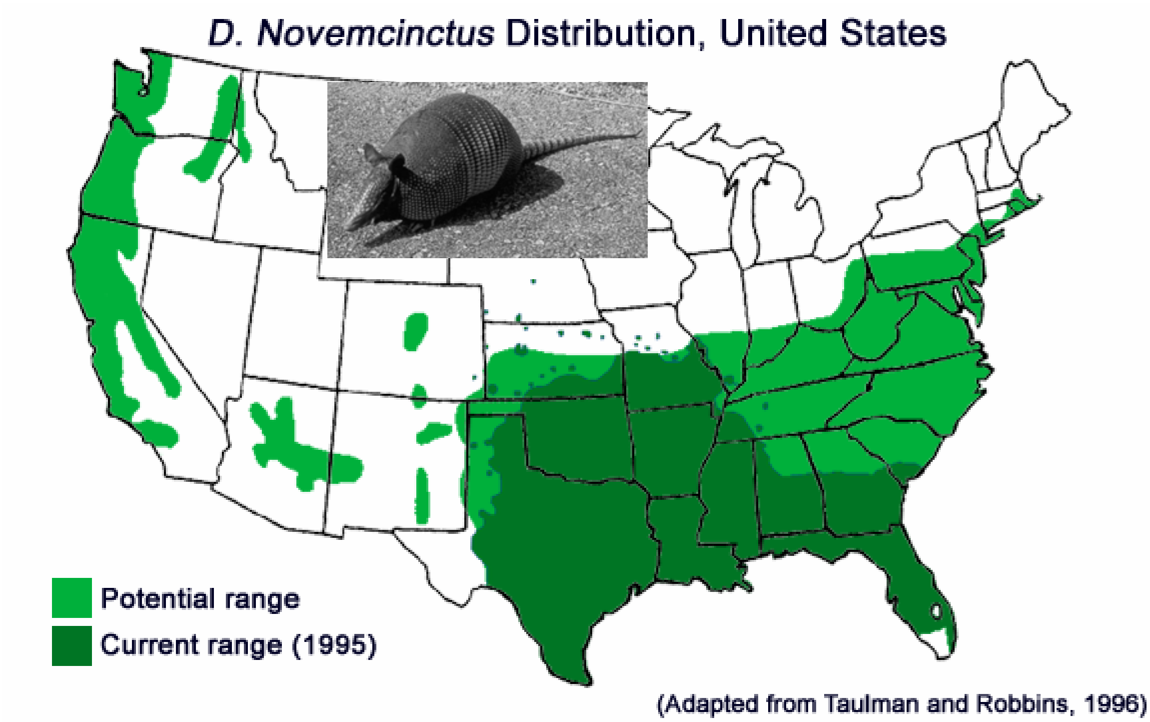



**Shown above is the relationship of Darwin's finches based upon combined cytb and cr sequences, demonstrating genetically the adaptive radiation that Darwin recognized visually in the Galapagos Islands in 1832 (Sato et al 1999).**

Islands were the birthplaces of many modern biogeographic ideas, but many of their endemic species are being threatened with extinction. As just explained above, some of the most important ideas and questions of modern biogeography were developed from studying islands and their endemic species, which are more numerous on islands compared to the mainland because of reproductive isolation. A case in point is the theory of evolution. During his trip to the Galapagos in 1832, Charles Darwin saw finches on different islands that led him to hypothesize that they all somehow descended from a common ancestor. This and numerous other such observations led him to propose the theory of evolution along with Alfred Russell Wallace, who also notably studied islands in Malaysia. Subsequent biogeographers continued to study when and how the ancestors of endemics first arrived, and how their subsequent reproductive isolation and exposure to new selective pressures drove their evolution into the unique species we see today.

Sadly, many of the unique assemblages of island species around the world that inspired early biogeographers like Darwin are now being threatened with extinction. Some of the most imperiled ecosystems in the world are island ecosystems, having suffered massive losses of their endemic species because of human activities or the introduction of invasive species (Loope and Mueller-Dombois 1989). Island endemics are highly sensitive to factors such as predation, trampling by herbivores, disease, and intense fires because they evolved in isolation from these forces, and are at a competitive disadvantage to continental species, which have endured these forces long enough to evolve adaptations to them (Loope and Mueller-Dombois 1989). These islands have become a major focus of biogeography in a different way, now that biogeographers are trying to address how to conserve these islands' endemic species.

3. The Nine-Banded Armadillo (*Dasypus novemcinctus*)




http://www.msu.edu/~nixonjos/armadillo/expansion.html

**The ecological niche of the nine-banded armadillo**

The nine-banded armadillo lives in diverse habitats that range from riparian forests to woodland savannas (Fitch 1952, Sikes et al 1990, Taulman and Robbins 1996). Woody habitats are important for armadillos because these omnivorous burrowing mammals forage in 10-12 cm of forest litter for their food (Taulman and Robbins 1996). They mostly eat invertebrates, with beetles and their larvae being the most common food item, but they are also known to eat eggs, small reptiles and amphibians, and some plant material, including cultivated crops (Fitch 1952). Beetles are most important in the summer and fall. Moths, butterflies, and dipterous flies in larval and pupal stages are more important in the spring, and reptiles and grasshoppers are important in the winter. Sikes et al (1990) found that fly larvae were also important in the winter, but concurred with Fitch's earlier finding that beetles and their larvae were eaten in all seasons except winter. Plant food is also important throughout the year, especially in fall. These consist of fleshy fruits, seeds, and mushrooms (Fitch 1952). However, plant material is less important to armadillos living in the northern part of their range compared to those living in the southern part; winter prey selection could reflect adaptations to harsher winter climates in the north, or to winter prey availability. (Sikes et al 1990)

The role of a species is an important component of its ecological niche, and Fitch (1952) provides information on the armadillos' beneficial and damaging roles. They benefit the ecosystem by destroying insect pests and dangerous snakes, digging burrows that are usable by other wildlife as nests and hiding places, and their digging in general mixes the soil and speeds the disintegration of dead wood. They have also benefited humans by becoming food for many rural people in Texas and other states. However, they also destroy crops, quail and domestic poultry eggs, and cause damage to buildings and livestock fences from their burrowing, which tend to make humans perceive them as less valuable.

Armadillos have small home ranges that average 2.5 ha and often overlap (Taulman and Robbins 1996). Layne and Glover (1977) suggest this small home range could reflect the species' specialization for feeding on small invertebrates, which pack a lot of energy and are found in higher biomass per unit area of landscape. Other carnivorous or omnivorous mammals that eat larger, more mobile, and sparsely distributed prey must range more widely to find them.

**Reasons for its expansion**

There are four main reasons for the rapid expansion of the armadillo's range: 1) climate warming, 2) human-induced environmental change, 3) human introduction of armadillos, and 4) omnivory.

<u>1) Climate warming</u>

Climate, particularly severe cold and dry weather, strongly restricts the armadillo's geographic range. Many reports of dead armadillos that could not find protective cover have been made following severe storms (Fitch 1952). This is because armadillos don't hibernate or store fat, so they must constantly forage for food (Merriam 2002). The heavy metabolic requirements during winter means a 5kg adult with 14% body fat can survive in a 0 degree C burrow for only 10 days; juveniles fare worse, with 2 kg juveniles having 10% body fat surviving for only 4 days (Humphrey 1974). Thus, Humphrey surmised that armadillos would be limited to regions with at least 38 cm annual precipitation and <9 freeze days/year.

However, the expansion was set to continue, due to a regional warming trend in the Great Plains (Humphrey 1974). Since the 1970s, armadillos have moved beyond regions with <9 annual freeze days, and have established in areas with 20-24 nonconsecutive annual freeze days and mean January temperatures > -2 degrees C (Taulman and Robbins 1996). Interestingly, this warming trend may have began decades before it was identified by Humphrey. Back in 1939, Taber claimed that "the occasional occurrence of cold weather in the vicinity of the 33rd parallel will probably prevent any great number of armadillos from becoming established north of this line." However, armadillos continued to migrate north after 1940, so winter temperatures must have warmed during that time. Thus, we see that a long history of warming in the southern and central US has allowed armadillos to survive farther and farther north.

Precipitation is also an important limiting factor. The annual precipitation limit is 38 cm; anything lower than that precludes the species' successful establishment or persistence in an area (Taulman and Robbins 1996). They state that armadillos may have already approached a precipitation-defined boundary in the west, one which was first identified by Humphrey (1974). In the east, since the species' precipitation and temperature boundaries lie far to the north, Taulman and Robbins claim that armadillos may continue to spread to 39 degrees N latitude in the Midwest, and 41 degrees N along the East Coast.

<u>2) Human-induced Environmental Change</u>

Since the climate warmed after the last glacial retreat, why didn't the armadillo invade the US long ago? There must have been non-climatic factors that limited its range. Before the mid 1850s, armadillo dispersal is believed to have been hindered by native subsistence hunters, the Rio Grande, and fire-maintained grassland barriers; these barriers were removed when southern Texas was settled by Europeans after 1850 (Taulman and Robbins 1996). The reduction or extermination of large carnivores in the Southwest by cattle ranchers meant that armadillo numbers were no longer kept in check by predation (Taber 1939, Sikes et al 1990). These predators would have included the red wolf, coyote, black bear, puma, jaguar, ocelot, and bobcat. Native Americans also hunted armadillos north of the Rio Grande, but their populations, along with the large predators, also declined upon European settlement (Taulman and Robbins 1996).

Also cited have been changing land-use patterns such as timber cutting, crop establishment, and livestock grazing (Fitch 1952, Sikes et al 1990). These changes have altered the ecosystem in the northern part of the armadillo's range, decreasing the extent of less suitable dry, fire-maintained grasslands, and increasing the extent of more suitable woody habitat (Taulman and Robbins 1996).

3) Human Introduction of Armadillos

Layne and Glover (1977) argue that the armadillo's spatial activity hasn't made a strong contribution to its range expansion, since they have small home ranges, low dispersal tendencies, and sedentary habits. Though armadillos have spread across vast distances, they demonstrated that their actual invasion rate has been slow, and attributed their spread to the accidental or deliberate introduction by humans.

The accidental and deliberate transportation of armadillos into new areas, such as from Texas to Louisiana, Mississippi, and Florida, has occurred hundreds of times across the south, and their dispersal rate was accelerated due to human travel and commerce (Fitch 1952, Taulman and Robbins 1996). Indeed, the steady growth of transportation routes coincides with the known beginnings of the armadillo's expansion, an interesting example of human range expansion facilitating the range expansion of another species.

4) Omnivory

Merriam (2002), in describing the successful northward migration of armadillos into Kansas, cites not only the warming climate and few natural predators as important reasons, but also the armadillo's omnivory. Omnivory is a quality that makes the armadillo a highly adaptable species. They have expanded their range into new, diverse types of habitat, and have had to alter their diet because of varying food availability. They will easily eat whatever is available during the season, and armadillos in the northern part of their range will consume a greater quantity of high-energy insects and less plant material during the winter than those in more southern portions of the range (Sikes et al 1990).

## Biogeographic History

The nine-banded armadillo was historically found south of the Rio Grande, its range limit being the lower Rio Grande Valley, near the Mexican border (Taber 1939, Fitch 1952). Several archaeological records show that they occupied Central America in prehistoric times, and today, this species has an extensive distribution in the American tropics (Humphrey 1974). However, Humphrey (1974) identifies Baird as having described a geographic range for the armadillo in extreme southern TX as early as 1859. Since its successful establishment on the US side of the Rio Grande, the armadillo has been gradually spreading northward and eastward. Humphrey predicted that armadillos would overtake their northern barrier in N. OK and AR or southern KS and MO. As of 1982, they occurred in limited numbers as far north as SW Missouri, southern KS, and extreme SE Colorado (Sikes et al 1990). In 2002, Merriam reported that armadillos have been found in almost 25% of KS counties, and are as far north as the Platte River in southern NE. Overall, their average invasion rate has been an extremely rapid 4-10 km/yr, owing to human introductions (Merriam 2002).

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