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Differential Mortality and the Donner Party Disaster

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The story of the Donner Party combines powerful American themes. The beginning of the tale is immersed in the romance of the western frontier and in the American dream of improving life by taking bold steps. The end of the tale, in contrast, is awash in death and cannibalism. No wonder Americans learn the story as children; no Grimm's fairy tale can match it. However, detailed analyses of the patterning of Donner Party deaths suggest that the story is even better read as a piece of biology than as a piece of history. Virtually all aspects of Donner Party mortality can now be explained by our knowledge of the factors that cause differential mortality in human societies. The differential fates of these emigrants show us natural selection in action.

In 1845, Lansford W. Hastings published a remarkable piece of propaganda. *The Emigrant's Guide to Oregon and California* was not, as the title might lead the unwary to assume, an impartial discussion of the overland routes heading west from what was then the United States. This was a book with a purpose: to lure emigrants away from Oregon and to California. The route to Oregon from Fort Hall, in what is now southern Idaho (Fig. 1), was, said Hastings, "but one continued succession of high mountains, stupendous cliffs, and deep, frightful caverns." In contrast, the road to California "lies through alternate plains, prairies, and valleys, and over hills, amid lofty mountains."¹ How foolish it would be to risk material goods and life itself to reach Ore-

gon when wondrous California was so much easier a target.

Prior to the publication of Hastings' book, three attempts had been made to take wagons across something resembling his "California route." In the attempts of 1841 and 1843, the people arrived safely but the wagons were left

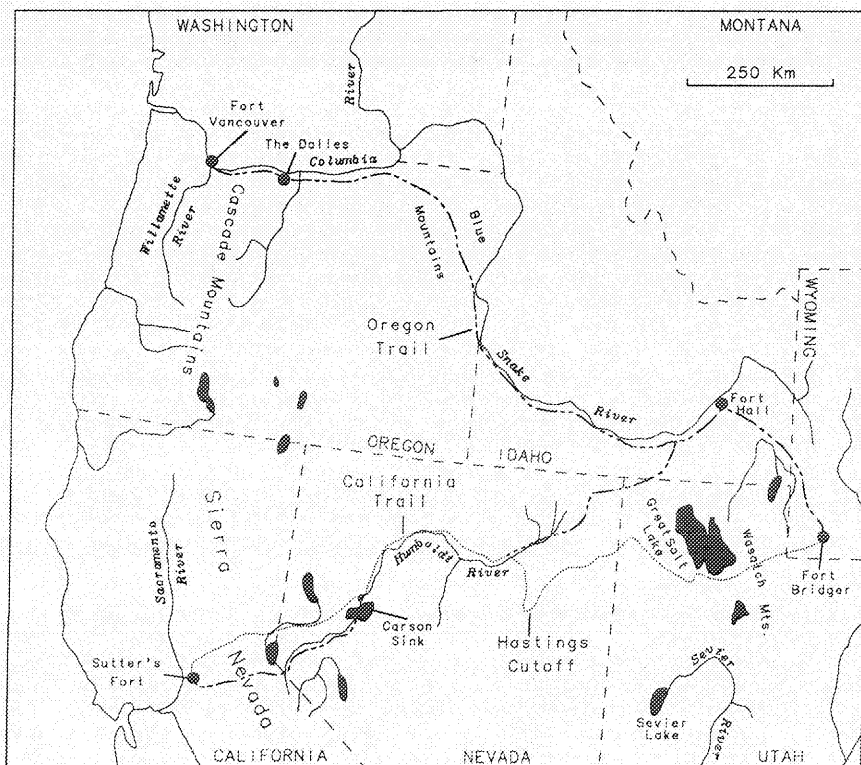
on the trail. In 1844, the Stevens Party negotiated some of their wagons across the Sierra Nevada, but the effort required was enormous. The party reached what is now Donner Lake on the east slope of the mountains in mid-November, but the last of the group did not reach the Sacramento Valley until March 1, 1845.²

The most famous of those who took what came to be called the California Trail, however, were not these vanguard pioneers, but those who followed soon after, drawn in by Hastings. This is the group now referred to as the Donner Party.

THE DONNER PARTY ROUTE

In mid-April 1846, 22 people be-

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Figure 1. Overland trails to Oregon and California during the 1850s; the Donner Party route is indicated by the dotted line.

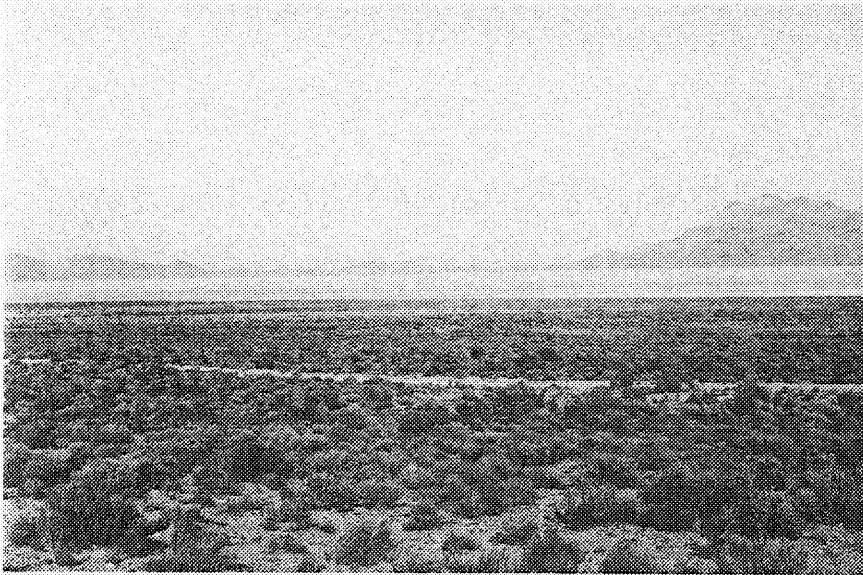


Figure 2. Donner-Reed Pass (center) from the eastern flank of the Pilot Range, on the Utah-Nevada border (see Fig. 1 for location). This pass led the Donner Party out of the Great Salt Lake Desert, where they had lost four wagons and dozens of animals.

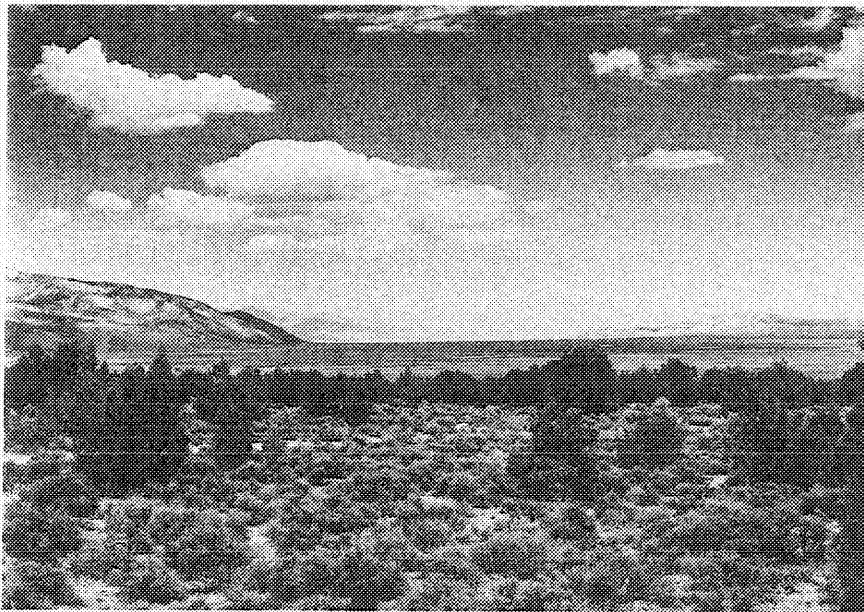


Figure 3. Ruby Valley and the eastern edge of the Ruby Range from the southernmost point of Hastings' cutoff; here, the Donner Party found ample water but at the cost of extra time spent on the trail (see Fig. 1 for location).

longing to three families—those of George and Tamsen Donner, Jacob and Elizabeth Donner, and James and Margaret Reed—left Springfield, Illinois, heading west for a new life. By July 27, they had reached Fort Bridger in southwestern Wyoming, where they made the final decision to follow Hastings' route to California. Leaving July 31, they headed west from Fort Bridger to enter the Wasatch Range of northeastern Utah. Here, the party

reached its full size: 87 people, 20 wagons, and a wide array of livestock. It was also here that they encountered their first significant difficulties, since the Wasatch Range presented a series of narrow, rugged canyons filled with dense vegetation. Cutting a road through thick aspen, willows, and shrubs, the group finally emerged into Great Salt Lake Valley on August 22. A critical three weeks had been spent traversing what they had believed

would be a shortcut.

After passing south of Great Salt Lake, the party had to cross the Great Salt Lake Desert, some 130 waterless and often salt-encrusted kilometers. The quickest of them made it in three days, the slowest in four, but the crossing took its toll. Four wagons had to be abandoned, an estimated 36 cattle were lost, and a week was spent reorganizing and recuperating at the eastern base of the Pilot Range on the Utah-Nevada border (Fig. 2).³

From here to the Sierra Nevada it was, finally, smooth sailing. Following another of Hastings' shortcuts, the group headed south along the east flank of the Ruby Mountains (Fig. 3), then north along the west flank of the same range. At this point, they met the Humboldt River, which they followed to its sink in western Nevada. From Humboldt Sink, they headed directly to the Sierra Nevada, the last great impediment between them and Sacramento Valley.

By now, however, it was late October, and it was too late for them. Moving up the east flank of the Sierra Nevada, they encountered snows of such depth that they were unable to either go forward or turn back. By November 1, they had established two camps, one adjacent to Donner Lake, another about 8 km to the northeast.⁴ Not until April 21, 1847 was the last survivor rescued. By then, however, 40 of the 87 had died, 35 as a direct result of the forced encampment in the Sierran snows.

THE DEMOGRAPHIC STRUCTURE OF THE DONNER PARTY

Because of the intense interest generated by their ordeal, a good deal of information on the geographic origin, age, and sex of the members of the Donner Party is available, much of which was recorded during the nineteenth century. It is known, for instance, that of the 87 people involved, 47 came from Illinois, 16 from Missouri, and 10 from Iowa. The sex of each individual is known, as is the age, or an estimate of the age, of all of the party members except one.

As a result, it is possible to compare the distribution of age and sex in the Donner Party to that in the population from which this sample of emigrants

TABLE 1. Age and Sex Distribution of "White" Illinois Residents in the 7th U.S. Census by 7th Census Age Class

Age Class	Total	%	% Male	% Female
1-4	141,360	16.72	49.11	50.89
5-9	129,905	15.37	48.88	51.12
10-14	112,860	13.35	48.11	51.89
15-19	92,698	10.97	49.34	50.66
20-29	150,044	17.75	47.03	52.97
30-39	102,426	12.12	44.17	55.83
40-49	62,072	7.34	44.60	55.40
50-59	33,828	4.00	43.47	56.53
60-69	14,410	1.71	44.69	55.31
70-79	4,577	0.54	44.79	55.21
80-89	938	0.11	46.27	53.73
90-99	109	0.01	49.54	50.46
100+	15	0.00	33.33	66.67

was drawn. Table 1 shows the number of "white" residents of Illinois by age class as reported in the 1850 (7th) United States census, as well as the distribution of males and females across those age classes. Table 2 provides comparable data for the Donner Party. (Details of some of the following analyses have been presented elsewhere,⁵ but here I have revised the ages of Patrick Breen and Mrs. Wolfinger using new information provided by King.⁶)

Statistical analysis of these data shows that the general age structures of the Donner Party and the "white" population of Illinois in 1850 are quite similar. However, individuals between 15 and 19 years of age are slightly under-represented in the Donner Party, and those between 20 and 29 years are slightly over-represented (both at $p = 0.06$).

There are no significant differences between the 1850 population of Illinois and the Donner Party in the distribution of females across age categories. Males, however, are greatly over-represented among the emigrants. This over-representation is highest for males between 60 and 69, because of the presence of George (62) and Jacob (65) Donner, but it is also pronounced for men between 20 and 39 years of age. This surfeit of men is no surprise, for men constituted a disproportionate number of western emigrants in general.⁷ In fact, while the proportion of Donner Party males between 20 and 39 years of age

(70.0%) is far higher than that in the population from which these males were drawn (45.9%), it is almost identical to the proportion of "white" males in Oregon in 1850 (72.9%). Although the proportion of young men in the Donner Party was distinctly different from that in the population from which these people came, it was distinctly similar to that in the population toward which it was heading.

PREDICTING DONNER PARTY DEATHS

As I mentioned, 40 of the 87 members of the Donner Party died after the group had reached its full size in the Wasatch Range. Of these deaths, 35 occurred after the winter camps had been established in the Sierra Nevada. Although there is no way of knowing the precise cause of death in these 35 cases, cold or starvation or both were clearly to blame. Given that the party consisted of 53 males and 34 females ranging in age from 1 to 65, traveling either alone or in family groups of variable size, can we use general patterns of human mortality to predict who should have died and who should have survived?

THE WEAKER SEX

"Frailty," said Hamlet, "thy name is woman." Measured in terms of mortality, however, frailty is a decidedly male attribute: in most contemporary settings, males die younger than females. In the 35 developed countries

analyzed by Lopez,⁸ a newborn girl can anticipate an average of 6.4 more years of life than a newborn boy, the difference ranging from 3.9 years in Albania to 10.0 years in the Soviet Union. In Africa as a whole, female life expectancy exceeds that of males by 6.8%.⁹ In the United States in 1980, newborn girls could expect to live 77.5 years, 7 years more than newborn boys.¹⁰ The sex differential in mortality has increased dramatically in developed countries during the twentieth century. In the United States in 1920, this differential was on the order of 2 years, a figure identical to that for Colombia in the mid-1960s.¹¹⁻¹⁵ However, the differential itself is not a modern phenomenon. For instance, females also outlived males in mid-nineteenth century America (Table 1). Although it is too much to claim that "women outlive men . . . in all societies"¹⁶—India, for instance, is a contemporary exception¹³—this statement is at least as accurate as the generalization that, in hunter-gatherer societies, it is the men who hunt and the women who gather.^{17,18}

Not only can males expect to have shorter lives than females, but they can also expect to have higher mortality rates at every age, including infancy.^{10,14,19} They may even die in greater numbers before birth, although the evidence for this is in dispute.^{14,16,20,21} Almost no matter where we look, males are at a longevity disadvantage compared to females.

This difference stems from a diverse set of proximate causes. Males die at a much greater rate than do females from ischemic heart disease,^{14,16,22,23} homicide,²⁴ suicide,¹⁰ motor vehicle and other accidents,^{8,25} and a wide variety of infectious diseases, including pneumonia, influenza, and septicemia.^{11,19,26} Males are even more susceptible than females to hookworm infection.²⁷ Indeed, it turns out that human males drop like flies. In fact, they drop very much like house flies (*Musca domestica*), one of many other species in which females outlive males.²⁸

Efforts to understand why these proximate causes differentially remove males continue.²⁹ It is clear, however, that biology is behind nearly all of the longevity gap. Biochemical

TABLE 2. Distribution of Males and Females in the Donner Party by 7th Census Age Class

Age Class	N of Males	N of Females	%	% Males	% Females
1-4	7	9	18.61	43.75	56.25
5-9	7	4	12.79	63.64	36.36
10-14	8	5	15.12	61.54	38.46
15-19	2	2	4.65	50.00	50.00
20-29	15	7	25.58	68.18	31.82
30-39	6	2	9.30	75.00	25.00
40-49	2	4	6.98	33.33	66.66
50-59	2	1	3.49	66.66	33.33
60-69	3	0	3.49	100.00	00.00
?	1				
TOTALS	53	34			

differences have, for instance, been implicated in the greater male susceptibility to both ischemic heart disease and infectious disease.^{11,12,14-16} In addition, in a study of mentally retarded adults who had had the misfortune of being institutionalized at a time when castration was considered an acceptable method of controlling behavior, Hamilton and Mestler found that the life expectancy of castrated males was 13.6 years greater than that of intact males.³⁰

Those who study the sex differential in human mortality routinely distinguish between biological and behavioral causes of that differential. Some even argue that if the behavioral causes were eliminated, little difference would remain between the age-specific mortality rates of the sexes.¹⁹ In addition to tobacco smoking, these arguments target homicide, suicide, and accidents, especially motor vehicle accidents, as behavioral causes of death among males.

On the other hand, a substantial body of anthropological, biological, and psychological literature suggests that many of the differences that are drawn between behavior and biology in this realm are artificial. Risk-taking and aggressive behavior are almost universal male attributes. Cross-cultural studies show that even though levels of male aggression vary substantially from society to society, young boys are routinely more aggressive than young girls within particular societies.³¹ In addition, females routinely participate in activities that are low in risk compared to those males

engage in, just as predicted by evolutionary biology.³²⁻³⁶ Insofar as these differences are caused by sex hormones,³⁷⁻⁴⁰ the sex differential in mortality resulting from such events as automobile accidents, homicides, and suicides is as biological in origin as biochemically-induced ischemic heart disease.¹⁶ The argument that without gender differences in behavior, the sex differential in mortality would not exist, differs little from arguing that if the sexes were the same, mortality would be the same.

Under usual conditions, then, males are shorter-lived than females and suffer greater mortality across all age classes. What might be expected to happen to this basal pattern under conditions of famine and extreme cold?

Once again, the advantage seems to go to females. Rivers has pointed out that a series of factors should make females less vulnerable to starvation than males: they are smaller (by approximately 17% of body weight⁴¹); they have a higher percentage of body fat (roughly 27%, compared to about 15% in males, though the absolute figures vary from population to population);^{42,43} and, after about the age of five years, they have a lower basal metabolic rate. As a result, males have higher nutrient and energy requirements than do females. Stini, for example, noted that a 70-kg man engaged in moderate physical activity will expend about 300 kcal per hour; 60 kcal more than a woman engaged in the same level of activity.⁴⁶ In addition, males use a greater proportion of

body protein to meet energy requirements than do females.⁴⁷

All other things being equal, it follows that females, especially adult females, should be more robust in the face of starvation than males, especially adult males, should be. Rivers argues that a higher proportion of females than males may die in any given episode of famine because of "male discrimination" against them.^{44,45} Because they are larger and more aggressive, men gain differential access to resources, thus reducing their mortality while increasing the mortality suffered by women. In situations in which both sexes share resources, starvation-induced mortality should differentially remove males from any given human population.

Of the many factors that may play a role in causing differential responses to cold by males and females, subcutaneous fat and body mass seem to be the most important, although regulatory differences stemming from the hypothalamus may also play a role.⁴⁸

Not only do women have a higher proportion of body fat, but a larger proportion of that fat is distributed subcutaneously. For instance, in a study of 214 Japanese men and women, Hattori and his colleagues found the women to have a greater absolute amount of fat (11.4 kg average, compared to 7.7 kg for men), a greater relative amount of fat (20.9% versus 12.4%), and a higher proportion of fat distributed subcutaneously (62.6% versus 53.7%).⁴³ Poorly vascularized, subcutaneous fat is an effective insulator. Accordingly, several studies have shown that when inactive individuals are exposed to cold, those with greater amounts of subcutaneous fat undergo smaller reductions in core temperature and smaller increases in metabolic rate.⁴⁹⁻⁵³

Women also maintain a lower skin temperature in response to cold than men do. It is frequently maintained that this difference is a result of the greater insulation provided by body fat,^{53,54} but not all studies support this conclusion.⁵⁵ No matter what the explanation, however, women's lower skin temperature decreases the temperature differential between body surface and air temperatures, and thus decreases the rate at which body heat is lost.

TABLE 3. Donner Party Members: Sex and Survivorship by 7th Census Age Class

Age Class	Males: Survived?			Females: Survived?			Totals	% No
	Yes	No	% No	Yes	No	% No		
1-4 (1) ^a	2	5	71.4	4	5	55.6	16	62.5
5-9 (2)	5	2	28.6	4	0	0.0	11	18.2
10-14 (3)	6	2	25.0	5	0	0.0	13	15.4
15-19 (4)	1	1	50.0	2	0	0.0	4	25.0
20-29 (5)	5	10	66.6	6	1	14.3	22	50.0
30-39 (6)	2	4	66.6	2	0	0.0	8	50.0
40-49 (7)	1	1	50.0	1	3	75.0	6	66.7
50-59 (8)	1	1	50.0	1	1	100.0	3	66.7
60-69 (9)		3	100.0				3	100.0
?		1					1	
TOTALS	23	30	56.6	24	10	29.4	87	45.0

^aNumbers in parentheses used to identify age classes in Figure 6.

While the amount and distribution of body fat work in favor of females, body mass would seem to have the opposite effect. Body mass tracks muscle mass, and muscles produce heat when active. As a result, larger-bodied individuals not only have greater thermal inertia, but can also produce more heat than smaller-bodied individuals. In addition, smaller people have a greater surface area/mass ratio; as a result they can lose more heat to the environment than can larger people. Accordingly, it has been argued that women are at a great disadvantage in the cold.⁵⁶ Nonetheless, empirical studies have repeatedly shown that under cold conditions, men undergo greater core temperature reductions than do women while maintaining higher skin temperatures, making it fairly clear that men are at a disadvantage in cold settings.

What of the old and very young? In normal situations, relatively high death rates characterize both the oldest and youngest members of human societies. Mortality is generally high between the ages of 1 and 5 years, then it decreases; above the age of about 35 it begins to rise, becoming increasingly higher among older adults.⁵⁷

Conditions of famine or cold, or both, exacerbate this pattern. Young children and older adults routinely suffer greater mortality under starvation conditions than they do when nutrition is adequate,⁴⁵ and a variety of studies has shown that these same age groups are far more prone to death from hypothermia than are people of

other ages. Young children, for instance, have smaller nutrient and energy stores than do adults;⁴⁵ older people are metabolically less responsive to cold; they maintain higher skin temperatures in cold situations; and they are less able to respond to heat loss by vasoconstriction.^{51,58-61} The result is that high mortality among the oldest and youngest members of a human population is to be expected under conditions of famine or extreme cold, or both.

What does all this lead us to expect for the Donner Party? Clearly, we should expect that the oldest and youngest members of the group failed to survive. We should also expect that males died not only in greater numbers than females, but sooner.

DONNER PARTY MORTALITY

This, in fact, is exactly what happened. Table 3 provides death and survivorship statistics for the Donner Party by age class. Figure 4 shows mortality rates by age class. Three aspects of these statistics stand out dramatically. First, death fell most heavily on the youngest (ages 1-4, 62.5%) and oldest (ages 50-69, 83.3%) members of the group. In fact, of the nine people (five men, four women) who were 45 years old or older, only Patrick Breen (51) and James Reed (46) survived. Reed, significantly, did not have to deal with the rigors of the forced Sierran encampment. Expelled from the group on October 5 while the party was still along the Humboldt River,

Reed crossed the Sierra Nevada alone, well before the snows fell. Later, he assisted in the rescue attempts mounted from Sacramento Valley.

In general, whether male or female, Donner Party survivors were, on average, younger than those who died. Surviving females averaged 15.8 years of age, 6.1 years less than those who died; surviving males averaged 18.2 years of age, 6.2 years less than the average age of those who died (Fig. 5). The oldest and youngest members of the Donner Party, then, underwent severe attrition, just as expected from general considerations of human mortality.

In addition, and again as expected, death fell most heavily on the male members of the group. Of the 53 males, 30 (56.6%) succumbed, as compared to 10 (29.4%) of the 34 females. That is, males died at nearly twice the rate of females, and at higher rates across most age groups (Fig. 4).

Of the 40 deaths, five occurred before the Sierran encampment. Luke Halloran (25) died of "consumption," presumably tuberculosis, south of the Great Salt Lake on August 28. On October 5, James Reed was provoked into stabbing John Snyder (25), who died of the wound. It was for this reason that Reed was forced to leave the group. Mr. Hardkoop was denied passage in the wagons; 60 years old and forced to walk, he died on or soon after October 8 along the Humboldt River. Mr. Wolfinger (age unknown) was apparently killed by two fellow travelers

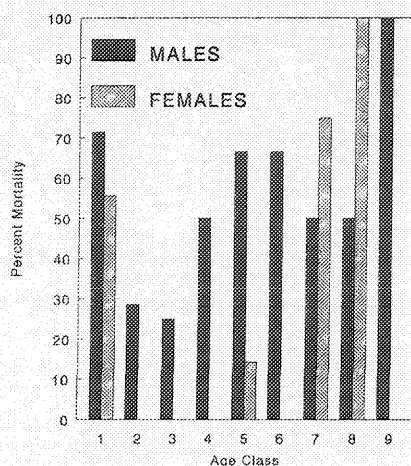


Figure 4. Donner Party mortality rates by age class (Table 3 provides the range in years for each numbered age class).

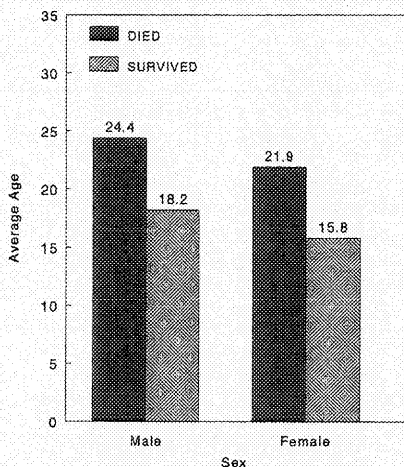


Figure 5. The average ages of Donner Party members by sex and survivorship status.

near Humboldt Sink on or about October 15; William Pike (25) was accidentally shot by his brother-in-law on October 20 while camped at Truckee Meadows, where Reno now sits. Five deaths, all and typically male: infectious disease, aggression, and violence.

Once in the Sierran encampment, not only did males die at far greater rates than females, but they also died more quickly than females. The Sierran camps were established about November 1. The first death among the forced campers occurred about six weeks later. The last occurred five months later, on April 1. First-hand accounts allow the timing of these deaths to be established either precisely or reasonably securely.^{6,62,63} As a result, a chronology of the deaths that occurred after encampment can be constructed. I have presented the raw data for this mortality timetable elsewhere.⁶⁴ Here I show the march of death and discuss why it looks the way it does.

Figure 6 displays the chronology of death across the 108 days during which Donner Party members died after the encampment. Males died not only in greater numbers than females, but sooner. The first 14 deaths, beginning on December 15 and continuing through January 30, involved only males. The first female, Harriet McCutcheon (1), succumbed on February 2, after which both males and females lost their lives.

An apparent oddity in this sequence

of deaths is the 18-day holiday that death took between January 6 and January 23. Before this lengthy interregnum, only males died; after it, both males and females died. In fact, of the 14 males who died before the first female death, 11 died during the 15-day interval that began December 15 and ended on December 29. During the next 33 days, only 3 additional males lost their lives. Why did the 18-day lull in deaths occur, and why did so many males succumb so quickly?

Figure 7 shows the relationship between age and days-to-death (treating December 15 as the first day-to-death) for all Donner Party males who reached the Sierran encampment. With one significant exception, age and days-to-death are inversely related among these males: the youngest tended to survive longest and the oldest died first.

The exception was 62-year-old George Donner. Donner had cut his hand badly in October, a wound that was never to heal. Once the Donner camp had been established, he could neither attempt to escape nor fend for himself. His wife, Tamsen, refused to leave with rescuers so that she could continue to care for her husband. With Tamsen's help, George survived until about March 26; Tamsen died the next day. George probably survived as long

as he did because of Tamsen's care and because he was not engaging in high-energy activities. Indeed, statistical analysis shows him to be a significant outlier (2.7 standard deviations) in the relationship shown in Figure 7. With or without George Donner, the rank order correlation (Spearman's rho, r_s) between age and days-to-death among the males is significant, but it is more significant without him ($r_s = -.67, p < .001$) than with him ($r_s = -.49, p = .013$). The average age of males who died before the lull was 32.4 years, and the average age of those who died after it, George Donner included, was 15.4 years. Among the males who died, George Donner was the only one to see the end of February.

Key to understanding both this relationship and the temporary cessation in mortality is the fact that both age and dependency were critical here. Of the 13 males who lost their lives after death had begun again, eight were dependent on others for their care, either because of their age (5 years or under) or because they were injured (George Donner). All of those who lost their lives during the first bout of death could fend for themselves.

And fend they did. First-hand accounts make it clear that it was the Donner Party men who bore the brunt

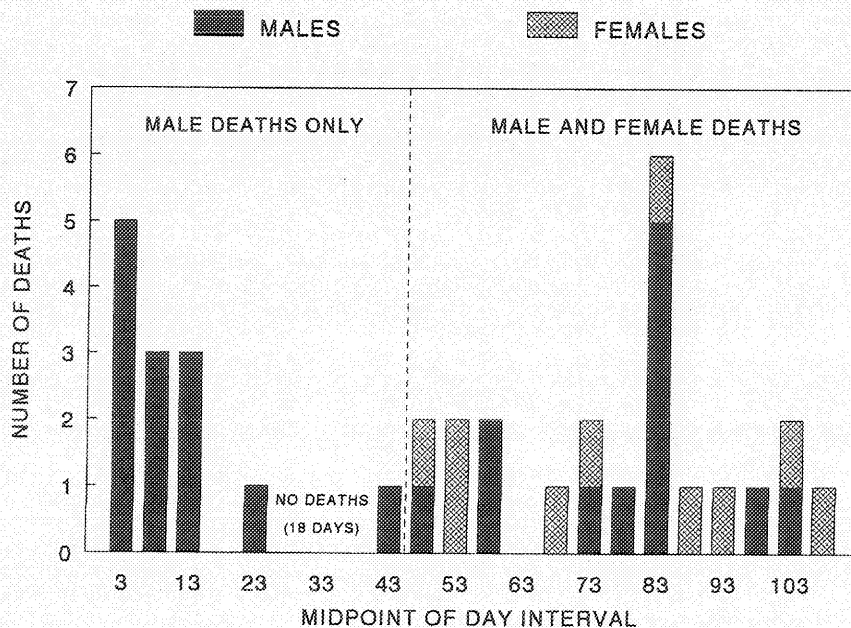


Figure 6. The march of death across Donner Party members who reached the Sierran encampment, by five-day intervals.

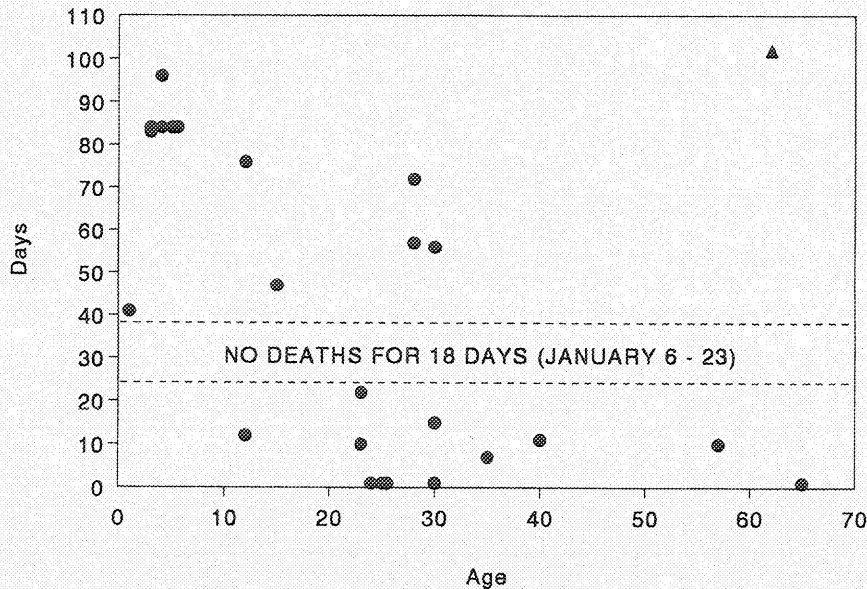


Figure 7. The relationship between age and days-to-death for the Donner Party males who reached the Sierran encampment; George Donner is indicated by the triangle in the upper right corner.

of the tremendous physical effort required for the group to negotiate the Wasatch Range, and who performed the heaviest chores in the Sierra Nevada. These, of course, are precisely the chores that males, by virtue of their biology, excel at performing and that, not coincidentally, they were expected to perform in mid-nineteenth century America. These men had certainly depleted their energy reserves in the Wasatch Range, a situation made worse once they were in the Sierra Nevada. Depleted, the adult males, including prime-aged individuals between 20 and 40 years, were the first to succumb. Once these men were gone, the first episode of death ended; 18 days later, the second episode, involving both males and females, began.

Thus, the initial round of deaths removed people who were doomed by their age and sex. The quick deaths of prime-aged men left the survivors largely without those whose duties would have included such tasks as hunting and wood-cutting. Without a full complement of vigorous adult males to accomplish these tasks, the survivors became far more dependent on rescuers than they otherwise would have been.

THE ROLE OF KIN GROUPS

One other factor was likely to have

been critical in determining differential mortality within the Donner Party. Diverse studies have shown that, under normal living conditions, longevity is positively correlated with the size of the social network within which an individual is embedded. This effect has been reported more consistently for men than for women.^{65,66} Although it is not clear why this effect exists, Berkman⁶⁵ has pointed out that a sense of belonging, access to information, and the availability of timely assistance all seem to play a role, and it is also possible that strong social networks strengthen immune systems.⁶⁷ There is no reason to think that the benefits of social networks would not have accrued to the members of the Donner Party, especially given the documented role that family and friends play in providing information and assistance in disaster settings.⁶⁸ It is also no surprise that accounts left by members of the Donner Party document that within-family assistance was routine. From this, it follows that mortality in the Donner Party might scale not only to age and sex, but also to the size of the family group in which each individual traveled.

Among individuals between 5 and 40 years of age, for whom age may be assumed to have had a lesser role in causing death, surviving males trav-

eled with families averaging 8.4 people. Males who did not survive traveled with families averaging 5.7 individuals. Surviving females of this age traveled with families whose size averaged 10.1 individuals; the one woman of this age who did not survive, Eleanor Eddy (25), traveled as part of a family of four. Larger kin groups seem to have provided life-enhancing support to members of the Donner Party.

If traveling with larger kin groups decreased the chance of dying, it might also have prolonged the lives of those who did die. Again, this seems to have been the case. The males who succumbed during the initial round of deaths were part of family groups whose size averaged 5.2 individuals; those who died during the second round traveled with families that averaged 9.9 members. As a whole, the chronology of deaths among the Donner Party males who reached the Sierran encampment is significantly, although perhaps not impressively, correlated with family size ($r_s = .53$, $p = .006$).

In the United States during the mid-nineteenth century, single women rarely traveled west on their own, while single men routinely made the journey. Within the Donner Party, there were 15 men, but no women, between the ages of 20 and 40 who were traveling alone. Of these 15 men, only 3 survived; nine had died by the time the lull in deaths occurred. Of the 13 males who died after death had resumed, 8 were children 12 years old or younger who, perforce, had to belong to family groups, while another was the dependent George Donner. Could the correlation between days-to-death and family size for males be caused by the early loss of prime-aged single men, coupled with the dependent status of many of those who survived the lull? If so, we would not expect to see a significant positive relationship between days-to-death and family size for females as well. This relationship, however, not only exists, but it is stronger than for males ($r_s = .724$, $p = .018$).

Family size thus appears to have played a significant role in mediating death among both the males and females of the Donner Party. The larger

the family with which a person traveled, the longer that person survived, many lasting long enough to either escape or be rescued. That family size played a greater role among the females is likely due to the fact that among males, the beneficial effects of being surrounded by family members were overridden by the losses of energy associated with the strenuous tasks they performed. That is, the benefits that male members of the Donner Party gained by belonging to increasingly larger family groups, they tended to lose by virtue of their sex.

CONCLUSIONS

Virtually all the deaths that occurred within the Donner Party can now be explained by what we know about general patterns of human mortality, differences between the sexes in resistance to cold and famine, and the role that social networks play in increasing longevity. Even the timing of Donner Party deaths can now be explained by this knowledge. Death fell most heavily on the youngest and oldest members of the group, on the males, and on those who traveled alone or with smaller support groups. Death came most quickly to prime-aged males, people who, by virtue of their biology, acted as they were expected to act. Death also came more quickly to those who, whether male or female, traveled with smaller support groups than it did to those whose support groups were larger. Far from simply illuminating the fate of a single, albeit famous, emigrant party, this knowledge confirms our understanding of some of the fundamental biological differences between human males and females, and provides us with a case study of natural selection in action within a human group.

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REFERENCES

- 1 Hastings LW (1845) *The Emigrants' Guide to Oregon and California*. Cincinnati: Conclin.
- 2 Grayson DK (1993) *The Desert's Past: A Natural Prehistory of the Great Basin*. Washington: Smithsonian Institution Press.
- 3 Hawkins BR, Madsen DB (1990) Excavation of the Donner-Reed Wagons. Salt Lake City: University of Utah Press.
- 4 Hardesty DL (1987) The archaeology of the Donner Party tragedy. *Nevada Hist Quart* 30:246-268.
- 5 Grayson DK (1991) Donner Party deaths: A demographic assessment. *J Anthropol Res* 46:223-242.
- 6 King JA (1992) *Winter of Entrapment: A New Look at the Donner Party*. Toronto: PD Meany.
- 7 Unruh JD Jr (1979) *The Plains Across: The Overland Emigrants and the Trans-Mississippi West, 1840-1860*. Urbana: University of Illinois Press.
- 8 Lopez AD (1983) The sex mortality differential in developed countries. In Lopez AD, Ruzicka LT (eds), *Sex Differentials in Mortality: Trends, Determinants and Consequences*, pp 7-32. Misc Ser 4, Department of Demography, Australian National University, Canberra.
- 9 Ohadike PO (1983) Evolving indications of mortality differentials by sex in Africa. In Lopez AD, Ruzicka LT (eds), *Sex Differentials in Mortality: Trends, Determinants and Consequences*, pp 33-52. Misc Ser 4, Department of Demography, Australian National University, Canberra.
- 10 Wingard DL (1984) The sex differential in morbidity, mortality, and lifestyle. *Ann Rev Public Health* 5:433-458.
- 11 Waldron I (1976) Why do women live longer than men? *Soc Sci Med* 10:349-362.
- 12 Seely S (1990) The gender gap: Why do women live longer than men? *Int J Cardiol* 29:113-119.
- 13 Heligman L (1983) Patterns of sex differentials in mortality in less developed countries. In Lopez AD, Ruzicka LT (eds), *Sex Differentials in Mortality: Trends, Determinants and Consequences*, pp 7-32. Misc Ser 4, Department of Demography, Australian National University, Canberra.
- 14 Waldron I (1983) Sex differences in human mortality: The role of genetic factors. *Soc Sci Med* 17:321-333.
- 15 Waldron I (1993) Recent trends in sex mortality ratios for adults in developed countries. *Soc Sci Med* 36:451-462.
- 16 Hazzard WR (1986) Biological basis of the sex differential in longevity. *J Am Geriatr Soc* 34:455-471.
- 17 Dahlberg F (1981) Introduction. In Dahlberg F (ed), *Woman the Gatherer*, pp 1-33. New Haven: Yale University Press.
- 18 Hawkes K (1993) Showing off: Tests of an hypothesis about men's foraging goals. *Ethol Sociobiol* 12:29-54.
- 19 Lancaster HO (1990) *Expectations of Life*. New York: Springer-Verlag.
- 20 McMillen MM (1979) Differential mortality by sex in fetal and neonatal deaths. *Science* 204:89-91.
- 21 Stinson S (1985) Sex differences in environmental sensitivity during growth and development. *Yearbook Phys Anthropol* 28:123-147.
- 22 Nathanson CA (1984) Sex differences in mortality. *Ann Rev Sociol* 10:191-213.
- 23 Short RV (1985) Species differences in reproductive mechanisms. In Austin CR, Short RV (eds), *Reproduction in Mammals, Book 4: Reproductive Fitness*, pp 24-61. Cambridge: Cambridge University Press.
- 24 Kellerman AL, Mercy JA (1992) Men, women, and murder: Gender-specific differences in rates of fatal violence and victimization. *J Trauma* 33:1-5.
- 25 Iskrant AP, Joliet PV (1968) *Accidents and Homicide*. Cambridge: Harvard University Press.
- 26 Dauer CC, Kornis RF, Schuman LM (1968) *Infectious Diseases*. Cambridge: Harvard University Press.
- 27 Schad GA, Anderson RM (1985) Predisposition to hookworm infection in humans. *Science* 228:1537-1540.
- 28 Rockstein M, Lieberman HM (1959) A life table for the common house fly, *Musca domestica*. *Gerontologia* 3:23-36.
- 29 Verbrugge AM (1985) Gender and health: An update on hypotheses and evidence. *J Health Soc Behav* 26:156-182.
- 30 Hamilton JB, Mestler GE (1969) Mortality and survival: Comparison of eunuchs with intact men and women in a mentally retarded population. *J Gerontol* 24:395-411.
- 31 Rohner R (1976) Sex differences in aggression: Phylogenetic and enculturation perspectives. *Ethos* 4:57-72.
- 32 Brown J (1970) A note on the sexual division of labor. *Am Anthropol* 72:1073-1078.
- 33 Lancaster JB (1985) Evolutionary perspectives on sex differences in higher primates. In Rossi AS (ed), *Gender and the Life Course*, pp 3-27. New York: Aldine.
- 34 Lancaster JB (1993) The evolutionary biology of women. In Almqvist AL, Manyak A (eds), *Milestones in Human Evolution*, pp 21-38. Prospect Heights, Illinois: Waveland Press.
- 35 Hawkes K (1990) Why do men hunt? Benefits for risky choices. In Cashdan E (ed), *Risk and Uncertainty in Tribal and Peasant Economies*, pp 145-166. Boulder: Westview Press.
- 36 Kaplan H, Hill K (1992) The evolutionary ecology of food acquisition. In Smith EA, Winterhalder B (eds), *Evolutionary Ecology and Human Behavior*, pp 167-202. New York: Aldine de Gruyter.
- 37 Meller R (1982) Aggression in primate social groups. In Marsh P, Campbell A (eds), *Aggression and Violence*, pp 118-136. Oxford: Basil Blackwell.
- 38 Ehrhardt AA (1985) The psychobiology of gender. In Rossi AS (ed), *Gender and the Life Course*, pp 81-96. New York: Aldine.
- 39 Moir A, Jessel D (1992) *Brain Sex: The Real Difference Between Men and Women*. New York: Dell.
- 40 Nicholson J (1993) *Men and Women: How Different Are They?* New York: Oxford University Press.
- 41 Harrison GA, Tanner JM, Pilbeam DR, Baker PT (1988) *Human Biology, Third Edition*. Oxford: Oxford University Press.
- 42 Wardle MG, Gloss MR, Gloss DS III (1987) Response differences. In Baker MA (ed), *Sex Differences in Human Performance*, pp 107-120. Chichester: Wiley and Sons.
- 43 Hattori K, Numata N, Ikoma M, Matsuzaka A, Danielson RR (1991) Sex differences in the distribution of subcutaneous and internal fat. *Hum Biol* 63:53-63.
- 44 Rivers JPW (1982) Women and children last: An essay on sex discrimination in disasters. *Disasters* 6:256-267.
- 45 Rivers JPW (1988) The nutritional biology of famine. In Harrison GA (ed), *Famine*, pp 56-106. Oxford: Oxford University Press.
- 46 Stimi WA (1981) Body composition and nutrient reserves in evolutionary perspective. *World Rev Nutr Diet* 37:55-83.
- 47 Widdowson EM (1976) The response of the sexes to nutritional stress. *Proc Nutr Soc* 35:175-180.
- 48 Graham TE, Viswanathan M, Van Dijk JP, Bonen A, George TC (1989) Thermal and metabolic responses to cold by men and

- eumenorrhic and amenorrhic women. *J Appl Physiol* 67:282-290.
- 49 Buskirk ER, Thompson RH, Whedon GD (1963) Metabolic response to cold air in men and women in relation to total body fat content. *J Appl Physiol* 18:603-612.
- 50 Sloan REG, Keatinge WR (1973) Cooling rates of young people swimming in cold water. *J Appl Physiol* 35:371-375.
- 51 Keatinge WR (1978) Body fat and cooling rates in relation to age. In Follinsbee LJ, Wagner JA, Borgia JF, Drinkwater BL, Gliner JA, Bedi JF (eds), *Environmental Stress: Individual Human Adaptations*, pp 299-302. New York: Academic Press.
- 52 Frisancho AR (1979) *Human Adaptation: A Functional Interpretation*. St. Louis: CV Mosby.
- 53 Haymes EM, Wells CL (1986) *Environment and Human Performance*. Champaign: Human Kinetics Publishers.
- 54 Wyndham CH, Morrison JF, Williams CG, Bredell GAG, Peter J, Von Rayden MJE, Holdsworth CD, Van Graan CH, Van Rensburg AJ, Munro A (1964) Physiological reactions to cold of Caucasian females. *J Appl Physiol* 19:877-890.
- 55 Graham TE, Loughheed TE (1985) Thermal responses to exercise in the cold: Influence of sex differences and alcohol. *Hum Biol* 57:687-698.
- 56 Burse RL (1979) Sex differences in human thermoregulatory response to heat and cold stress. *Hum Factors* 21:687-699.
- 57 Bogue DJ (1969) *Principles of Demography*. New York: John Wiley & Sons.
- 58 Wagner JA, Robinson S, Marino RP (1974) Age and temperature regulation of humans in neutral and cold environments. *J Appl Physiol* 37:562-565.
- 59 Collins KJ, Dore C, Exton-Smith AN, Fox RH, MacDonald IC, Woodward PM (1977) Accidental hypothermia and impaired temperature homeostasis in the elderly. *Br Med J* 1:353-356.
- 60 Scaman J, Leivesley S, Hogg C (1984) *Epidemiology of Natural Disasters*. Basel: Karger.
- 61 Wagner JA, Horvath SM (1985) Influences of age and gender on human thermoregulatory responses to cold exposures. *J Appl Physiol* 58:180-192.
- 62 Thornton JQ (1986) *Camp of Death: The Donner Party Mountain Camp, 1846-1847* (reprint of 1849 publication). Golden: Outbooks.
- 63 Stewart GR (1960) *Ordeal by Hunger: The Story of the Donner Party*. Lincoln: University of Nebraska Press.
- 64 Grayson DK (n.d.) The timing of Donner Party deaths. In Hardesty DL (ed), *Donner Party Archaeology*, in press. Reno: University of Nevada Press.
- 65 Berkman LF (1984) Assessing the physical health effects of social networks and social support. *Ann Rev Public Health* 5:413-432.
- 66 Kaplan RM, Toshima MT (1990) The functional effects of social relationships on chronic illnesses and disability. In Sarason BR, Sarason IG, Pierce GR (eds), *Social Support: An Interactional View*, pp 427-453. New York: John Wiley & Sons.
- 67 Kennedy S, Kiecolt-Glaser JK, Glaser R (1990) Social support, stress, and the immune system. In Sarason BR, Sarason IG, Pierce GR (eds), *Social Support: An Interactional View*, pp 253-266. New York: John Wiley & Sons.
- 68 Neal DM, Perry JB Jr, Green K, Hawkins R (1988) Patterns of giving and receiving help during severe winter conditions: A research note. *Disasters* 12:366-377.

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The Evolution of Primate Communities and Societies in Madagascar

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During their 120 to 165 million years of isolation, the flora and fauna of Madagascar evolved, to a large extent, independently of the African mainland.¹ In contrast to other oceanic islands, Madagascar is large enough to house the major components of tropical ecosystems, allowing tests of evolutionary hypotheses on the level of complete communities. Taking lemurs, the primates of Madagascar, as an example, evolutionary hypotheses correctly predict the organization of their community structure with respect to ecological correlates. Lemur social systems and their morphological correlates, on the other hand, deviate in some respects from those of other primates. Apparently, lemur social systems are influenced by several selection pressures that are weak or rare in other primates. These include variable activity patterns and avoidance of infanticide. The interspecific variation in lemur social systems therefore offers a unique opportunity for a comprehensive study of the determinants of primate social systems.

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MADAGASCAR: EVOLUTIONARY HISTORY AND BIOGEOGRAPHY

All Malagasy primates and the majority of other taxa are endemic.² Although many other islands share a high degree of endemism, Madagascar is exceptional in that it houses all major components of tropical ecosystems, including large carnivores.

Key words: Madagascar, Lemuriformes, community ecology, social evolution, sexual dimorphism

Because no other island harbors complete tropical ecosystems with such a high degree of endemism, Madagascar provides a unique opportunity to test hypotheses about evolutionary theory.^{3,4} Taking the primates of Madagascar (Lemuriformes) as an example, we have performed several crude tests of current hypotheses about the evolution of primate communities and societies.

The eastern and the western regions of Madagascar constitute two of the 20 centers of endemism recognized in tropical Africa.² The western region includes the spiny forests of the south and the deciduous forests along the west coast. The eastern region can be subdivided into the domains of the evergreen rainforest, the Sambirano, the region of the high mountains and the central high plateau (Fig. 1). Recent pollen analyses indicate that Madagascar was not covered by continuous forest before the arrival of man. Rather, the areas covered by the eastern and western forests expanded and retreated along with climatic changes,