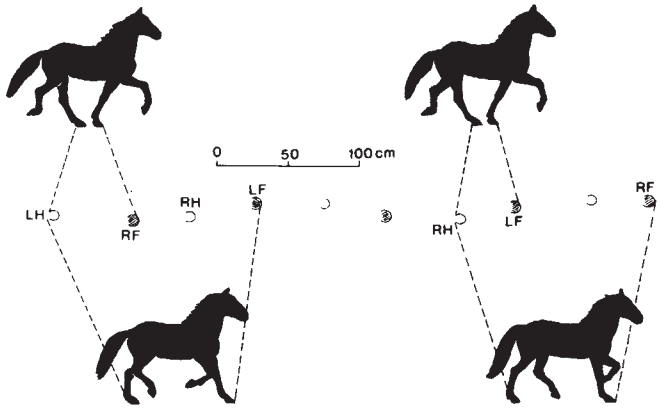

Fig. 3 The running walk: the four-beat alternation of diagonal and lateral leg support, in the sequence right front (RF), LH, LF and RH. The footprint pattern in the centre of the figure is trail *b* made by an adult *Hipparion*: its footfall sequence corresponds to that of a domestic horse travelling in running walk. The third horse from the left of the figure is in that stage of motion, corresponding to *Hipparion*, when it was sliding and being supported by the side toes of its right hind leg.

the footfall sequence the animal was sliding on its left fore foot, which left a broad and vague imprint (Fig. 3, third horse). The animal seems to have lost balance and compensated for this by the use of the opposite (diagonal) leg, (that is, the right hind leg) and shifting of the centre of gravity. This leg thus bore extra weight and was bent deeper through the fetlock of its main toe so that the side toes came in contact with the ground. The side toes, which were tightly attached to the main toe by ligamentous connections[14], prevented overextension of the fetlock of the main toe. In *Hipparion* the 'springing mechanism' (that is, the assemblage of tendons in the foot in which elastic energy can be stored[15]) was apparently not as fully developed as in the main toe of modern horses[16].

The fossil horse, however, had side toes, the elastic tendons of which could have actively contributed to the forward impulse. Hence, although the Laetoli soil was slippery due to the falling ash rain, *Hipparion* managed to balance itself and appears to have been able to pursue its route at constant speed. The importance of this analysis for understanding the evolution of equine gaits is twofold. The opinion that the running walk is an 'artificial and man-taught' gait is not supported by the results of this study. Young foals of several domestic breeds perform this gait in semi-wild conditions (E.R., unpublished observations), suggesting the ability to select this gait is a natural one in living equids.

Living horses are capable of selecting both lateral and diagonal gaits during locomotion, whereas most living mammals select only one or the other[17]. The more familiar diagonal gaits are the trot (a two-beat gait) and the transverse gallop (a three–four beat gait), but equids are also capable of selecting the lateral equivalent of these gaits, the pace and the rotary gallop (such gaits are typical of long-legged ungulates such as camels, giraffes and certain antelopes). The walk and the running walk contain a mixture of lateral and diagonal legs moving alternately, in a four-beat rhythm.

The results of the present study indicate that a diversity of gaits existed among the fossil forerunners of modern horses. It is uncertain why some horse breeds are able to use the full range of gaits.

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Reciprocal food sharing in the vampire bat

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Behavioural reciprocity can be evolutionarily stable[1–3]. Initial increase in frequency depends, however, on reciprocal altruists interacting predominantly with other reciprocal altruists either by associating within kin groups or by having sufficient memory to recognize and not aid nonreciprocators. Theory thus suggests that reciprocity should evolve more easily among animals which live in kin groups. Data are available separating reciprocity from nepotism only for unrelated nonhuman animals[4]. Here, I show that food sharing by regurgitation of blood among wild vampire bats (*Desmodus rotundus*) depends equally and independently on degree of relatedness and an index of opportunity for reciprocation. That reciprocity operates within groups containing both kin and nonkin is supported further with data on the availability of blood-sharing occasions, estimates of the economics of sharing blood, and experiments which show that unrelated bats will reciprocally exchange blood in captivity.

The primary social unit of the vampire bat is the female group. During a 26-month (September 1978–February 1983) study in northwestern Costa Rica, 184 of the estimated 200 *D. rotundus* encountered inside 14 hollow tree day roosts at one site were netted and uniquely marked with wing bands. Infants were matched to mothers by direct observation of nursing or parturition. Weekly roost censuses revealed that adult females can be assigned to one of three groups, each consisting of 8–12 adults and their dependent offspring, according to which trees they visit. Members of each group moved between 2–5 day roosts; subsets of 2–4 females and young often roosted in different trees. Each of 17 males which attained 1 year of age left their natal groups while all 11 yearling female offspring were recruited into their maternal groups. Consequently, female groups contain some close relatives. Exceptions are due to the recruitment of, on average, one unrelated female per group every 2 yr. I estimated relatedness between females from path analysis[5] of

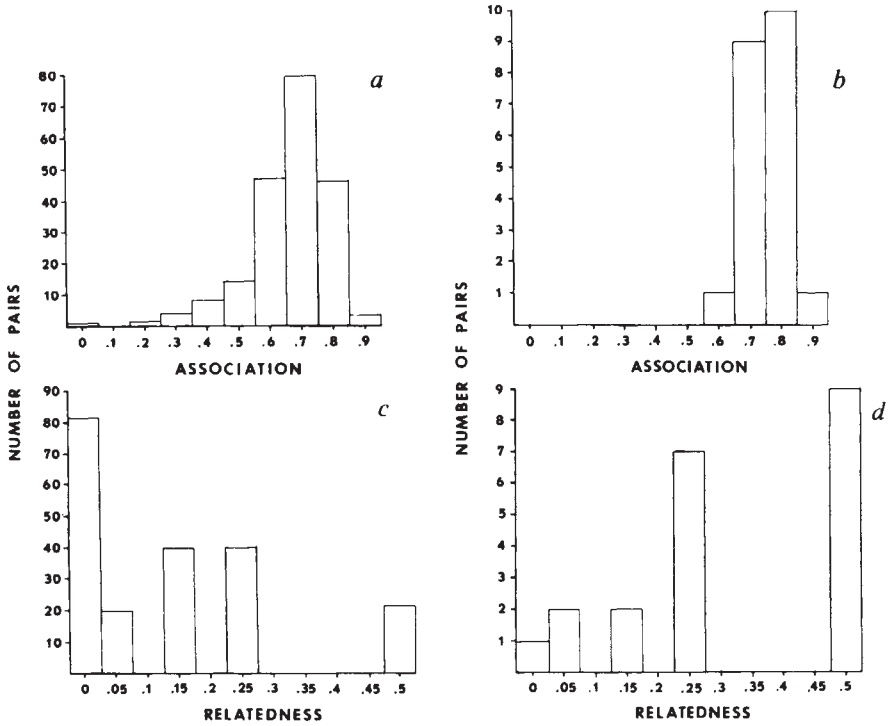

Fig. 1 Data used in the logit analysis. The recipient in each of 21 regurgitations in which mothers did not feed their nursing young was matched to all potential donors in the roost to obtain the frequencies of association and relatedness for potential donor–recipient pairs graphed in histograms *a* and *c*, respectively. The indices computed between blood-sharing pairs, tallied in panels *b* and *d*, indicate that regurgitations occur predominantly among frequent roostmates and close relatives. The significance of these patterns was determined with a stepwise logistic regression in which relatedness entered first ($\chi^2_1 = 25.6$, $P < 0.001$) and the association entered second ($\chi^2_1 = 9.0$, $P < 0.003$). Neither the interaction of relatedness and association nor a sampling effect variable, regurgitation number, had sufficiently low probabilities ($P < 0.1$) to enter into the regression[20]. Contingency table analyses showed that the frequency of regurgitation was independent of the age of either sex as well as the reproductive condition of females for both donors and recipients; however, females received blood more often than males ($\chi^2_1 = 5.58$, $P < 0.025$) even though donor sex was also independent of regurgitation frequency.

matrilineal pedigrees; observations and electrophoretic exclusion analyses indicated that paternity and inbreeding made negligible contributions to relatedness (manuscript in preparation). In the one group where pedigrees were extensive, the average coefficient of relatedness among adult females in 1981 was 0.11 (s.d. = 0.17, $n = 11$); estimates for relatedness (to be reported elsewhere) based both on electrophoretic data from other groups and simulations gave similar, but usually even lower, values.

During 400 daylight hours of focal animal sampling[6] within roosts, 110 cases of regurgitation (mean duration = 63.0 s, s.d. = 57.6 s) were observed. Seventy-seven of these feedings occurred between a mother and her nursing offspring. In 21 of the other 33 donations, the degree of relatedness and a measure of association[7], an index of opportunity for reciprocity, were known between the recipient and every other bat in the tree. (The association index is $2N_t/(N_1 + N_2)$ where N_t represents the number of times both bats were observed together until the day of regurgitation and N_i is the total number of times bat i was observed.) By logit analysis[8] of these data (Fig. 1) both relatedness and association significantly predict regurgitation independent of their correlation. The relative effects of the variables, as measured by the standardized regression coefficients[9] (-1.25, s.e. = 0.48, for association and -0.96, s.e. = 0.33, for relatedness), are approximately equal. These results indicate that regurgitations between distant relatives only occur between animals that have been frequent roostmates, as expected where reciprocity occurs. For reciprocity to persist among *D. rotundus*, however, three conditions[1] need to be fulfilled: (1) enough repeated pairwise interactions must occur to permit role exchanges and ensure that a net benefit accrues to all donors; (2) the benefit of receiving aid must exceed, on average, the cost of donating; and (3) donors must be able to recognize and not feed previous recipients that fail to reciprocate.

Several aspects of female *D. rotundus* natural history act together to create repeated opportunities for exchanging blood. Bats that fail to obtain a blood meal are usually fed by roostmates. Five of 8 bats captured before feeding and released into their roosts at dawn were subsequently given blood by a group member, whereas six bats captured at the same time but after

Table 1 Blood sharing among captive *Desmodus rotundus*

Starved bat	Donor bat(s)	Potential reciprocators*	Reciprocal feeding?	Probability of exchange†	
				Cage	Population
ROG(S)	OYR(S)	—	—	—	—
OO(L)	GB(L)	—	—	—	—
WB(L)	OO(L)	—	—	—	—
GB(L)	WB(L)	OO	No	4/5	2/3
OYR(S)	ROG(S)	ROG	Yes	1/7	1/3
YBR(S)	—	—	—	—	—
GRB(L)	WB(L)	—	—	—	—
ROG(S)	GRB(L)	OYR	No	5/6	—
OO(L)	WB,GB(L)	WB	Yes	1/5	1/3
WB(L)	GRB,GB(L)	GRB,GB	Yes	1/15	1/3
YO(S)	OYR(S)	—	—	—	—
GRB(L)	WB(L)	WB,ROG	Yes	2/7	1/3

Starved and donor bats are ordered according to the chronological sequence of blood sharing; population of origin is indicated in parentheses.
* Bats which have been fed by the recipient but have not yet returned any blood.
† The probability that the observed donation would occur with a potential reciprocator by chance given the number of potential donors either in the cage or from the same population. The combined binomial probability of witnessing as many or more such reciprocal exchanges, if any adult in the cage is considered a potential donor, is 0.009; if donors must come from the same population the probability is 0.045. Bat YBR was an adult male; ROG was near parturition; YO had a nursing infant; and GB was the grandmother of OO.

feeding received no blood when released ($P = 0.003$, binomial probability). Thus, reciprocal blood sharing can occur only if failure to obtain a blood meal is not synchronized in the population. The following shows that only age influences feeding success. At the main study site, La Pacifica, 23 of 121 bats, captured on 22 nights returning to roosts too late for additional foraging, weighed less than pre-fed weights determined on previous captures and were assumed therefore not to have fed. Using the same criteria at another study site, Santa Rosa, I found that 86 of 477 bats also failed to feed on 31 nights. Contingency table analyses using three-way G tests showed no effect of sex, population, reproductive condition or Moon phase on feeding success. But when population and sex categories are pooled, 33% of 258 bats less than 2 yr of age failed to feed while only 7% of the 340 older bats did not obtain blood meals ($G = 45.3$, $P < 0.005$). These data are not biased by a few repeatedly unsuccessful foragers; at both sites the frequency of unsuccessful feeding trips for individuals captured two, three or more times did not differ significantly from expected frequencies after controlling for age effects. When considered with the longevity of females and stable composition of groups, these data indicate that numerous opportunities both to share and to receive blood exist. Females as young as 8 months of age were observed to donate blood (personal observation) and can live for 18 yr[10]. Annual mortality is sufficiently low among adults (24%) for females to spend long periods together. For example, seven of the nine adult females present in one group in 1980 were still roosting together in 1982; in another group one pair of females marked by T. Fleming (personal communication) in 1970 roosted in the same area in 1981.

Vampire bats fulfill the second condition for reciprocity since their weight decays exponentially following a meal (Fig. 2*a* and ref. 11). To predict the time remaining to a fasting bat before death, weight loss attributable to post-feeding diuresis[12] can be subtracted from overall weight loss to produce a curve (Fig. 2*b*) which is due to metabolic and evaporative water losses. The concave downwards shape of this curve enables a donor to transfer weight by regurgitation and lose less time before reaching starvation than a recipient gains (Fig. 2*b*). The amount of blood transferred need not translate linearly into units of survivorship; it is sufficient that a blood donation increase the time until starvation sufficiently for a bat in need to forage at least once more. Observed blood transfers support this proposition. I estimated from a calibrated weights loss curve that one captive bat which received blood for 400 s gained about 12 h, assuming that fluid is transferred at drinking rates[13]. For comparison in the wild, one donation lasted 390 s.

The third condition for reciprocity requires that nonreciprocating bats can be identified and refused aid. I conducted experiments on captive animals which confirmed part of this requirement; unrelated but closely associated bats are capable of sufficient recognition to reciprocally exchange blood. The study group was created by housing four La Pacifica adult females from one roost tree with three adult females, one infant and one adult male from a cave 50 km away at Santa Rosa, in a cage 60 × 30 × 30 cm. No two bats shared a common ancestor for at least three generations except a grandmother–grandoffspring pair from La Pacifica. Association of females within populations was high but that between the male and females was low. To create a need for regurgitation, one bat was removed each evening before feeding and the remaining bats were given access to blood for 2 h. Two to twelve hours later the hungry bat was reintroduced and all ensuing interactions between individuals during the next 2 h were observed through an image intensifier with IR illumination and recorded. Each evening a different bat was chosen at random without replacement until every adult had been starved. All bats were starved at least twice during the experiment and both body and blood meal weights were recorded daily. Prior to the experiment weight loss curves such as shown in Fig. 2 were obtained for each adult bat and fitted with negative exponential functions to predict survival time.

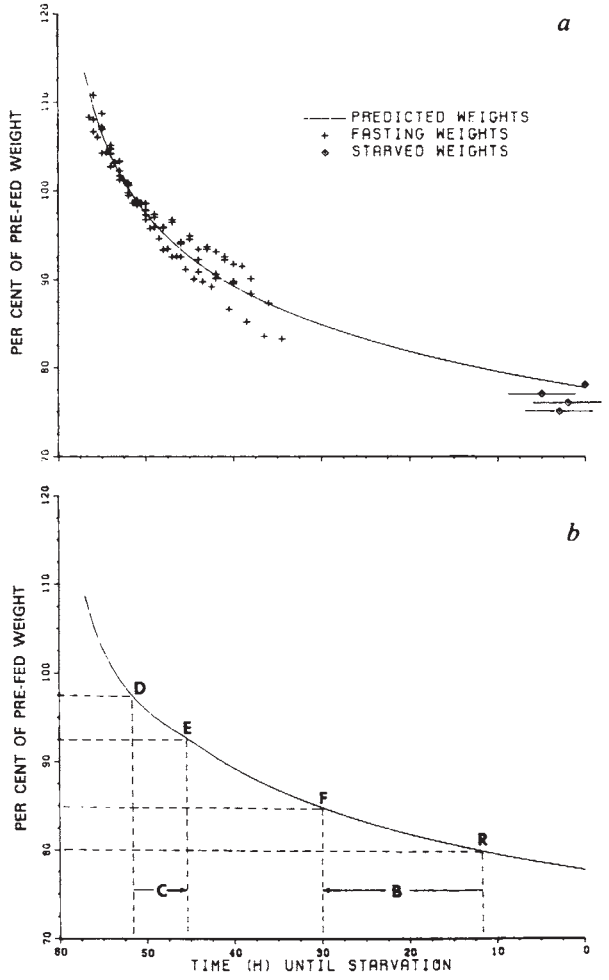

Fig. 2 Post-feeding (≥2 h) weight losses of one adult male and five adult female captive *D. rotundus* expressed as per cent of weight when captured at 1900 h (*a*). This weight was used as a referent because of its convenience and constancy; mean coefficient of variation for adult males captured three or more times was 2.85% (s.d. = 1.17, $n = 11$). To control for differences in meal sizes, the times elapsed since feeding that corresponded to each bat's 100% pre-fed weight (other values produced similar curves) were matched and a negative exponential function[11] ($W = 130.25t^{-0.126}$, $r^2 = 93.0$, $n = 82$, $P < 0.001$) was fitted by least-squares estimation. The weights of four bats that starved accidentally in a prior experiment were not entered in the regression but are included, with error bars to indicate uncertainty as to the exact time of death, in *a* to show the predictive ability of the function in the extrapolated region and that death does occur near 75% of pre-fed weight. Weight loss attributable to diuresis[12] 15 h post-feeding was subtracted from the fitted curve in *a* to obtain the predictive curve in *b*. Because fluid is absorbed in the stomach approximately at the rate that urine is excreted[13], blood meal consistency changes little 2 h after feeding. Therefore, a donation of 5% of pre-fed weight when at weight D should cause a donor to lose C h but provide B h to a recipient at weight R. The recipient benefit always exceeds the donor's cost when E > F.

Blood was donated preferentially to individuals in dire need from the same population. For each of the 13 observed regurgitations the recipient would have reached minimum viable weight in less than 24 h (mean 13.2 h, s.d. = 4.7 h), if it had not received blood. On the other hand, donors could have expected to survive at least 24 h (mean = 39.9 h, s.d. = 15.5 h). Consequently, trials in which the starved bat had received no blood and had more than 24 h left before starvation were excluded from the following analyses. Twelve of the 13 ($P = 0.002$, binomial probability) regurgitations (mean duration = 25 s, s.d. = 25 s) occurred between bats from the same population (Table 1). To test whether or not these feedings occurred independently of prior

blood sharing, each trial in which a donor fed a starved bat was compared with the subsequent trial in which the donor was starved. Starved bats which received blood later reciprocated the donation significantly more often than expected had exchanges occurred randomly (Table 1). These results do not depend on donors having more blood to share than nondonors. The rank of the donor with regard to its expected number of hours left before starvation was not significantly different from the median rank of bats within the cage or population ($P > 0.15$, Kolmogorov–Smirnov test). As expected, the only bat with low association, YBR male, was not fed even when in need. These results are very difficult to reconcile with any interpretation of food sharing based solely on kin selection.

Two recent reviews[14,15] overemphasize suspected instances of reciprocity which occur among unrelated animals. The results described here indicate that reciprocity can occur within groups that contain relatives. Further study of other food-sharing mammals[16–19] as well as other altruistically behaving animals which live in kin groups may reveal that reciprocity is more important in maintaining altruism than has previously been acknowledged.

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Bipolar cells in monkey retina selective for the cones likely to be blue-sensitive

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Bipolar cells are a class of retinal interneurone with dendrites in the outer plexiform layer that contact photoreceptors, and axons terminating in the inner plexiform layer[1] where they convey the centre responses of ganglion cells[2,3]. In the monkey, many of whose ganglion cells respond to stimuli selective[4] for each of the three different cones[5,6]. There are five types of cone bipolar cells: flat and invaginating midget[7–9]; diffuse, flat[7] and invaginating cone[7,10]; and giant, bistratified[11]. Although many of the monkey's ganglion cells are specific for one of the three different cone mechanisms, none of the bipolar cells are known to connect to the morphologically identified counterparts of the different spectral types of cones as in teleost retina[12–15]. Here, however, I describe a bipolar cell found in Golgi preparations of the rhesus monkey retina which displays an apparently selective and patterned distribution of its dendritic contacts with cone pedicles in the outer plexiform layer. The intercone spacing of dendritic contacts and their distribution match the intercone spacing and proportion of cones thought to be blue-sensitive[16,17].

Thirty-six retinas of 19 adult, male and female, rhesus monkeys (*Macaca mulatta*) were Golgi impregnated as described elsewhere[18]. Most neurones were observed in whole mounts in which there was no linear shrinkage. Selected cells were radially sectioned, and the preparations were studied by light microscopy. A bipolar cell type which appeared similar to invaginating midget bipolar cells was found. It possessed a small dendritic cluster, smaller than the diameter of a cone pedicle, and an axon that terminated low in the inner plexiform layer (IPL) (Fig. 1*a*). However, it displayed many distinct features. Several primary dendrites arose from the apical surface of the cell body and coursed horizontally through the outer plexiform layer (OPL) (Figs 1*a*, 2). Some of these converged at a distance from the axis of the cell body and axon, and at the level of cone pedicles formed a small cluster of coarse dendritic terminals (Figs 1*a*, 2) identical in span to that formed by the invaginating midget bipolar cells (3.5 μm in the most central regions and up to 7 μm in peripheral retina). At 5 mm eccentricity these clusters were composed of nine dendritic terminals ($n = 10 \pm 1.41$ s.d.) The individual terminal dendrites, although too small to be measured accurately with a conventional ocular reticle (<0.5 μm), appeared to be larger than those of the invaginating midgets. Some other dendrites of this new cell type ended wholly within the inner stratum of the OPL and did not contact any photoreceptor terminal (Figs 1*a*, 2). In the IPL, the axon descended to the innermost stratum adjacent to the ganglion cell layer, where it terminated as an elongate structure, with few branches, and with a total span ranging from central to peripheral retina of about 20–50 μm (Fig. 1*a*). Although this terminal arborization was broad in span, it was narrowly stratified in the innermost stratum of the IPL, and while ending in close proximity to the ganglion cell bodies, these axon terminals did not appear to touch or insert themselves between these cell bodies as did the axon terminals of rod bipolars[7]. Invaginating midget bipolar cells, however, had a single main dendrite which terminated in a 'bouquet'[7] (Figs 1*b*, 2). At the same eccentricity (5 mm) where the newly identified bipolar cells had an average of nine dendritic terminals the 'bouquets' of invaginating midget bipolar cells had 19.8 dendritic terminals ($n = 10 \pm 3.31$ s.d.). Additionally the axon terminal of the invaginating midget bipolar cell, which ended in the inner half of the IPL, was broadly stratified but did not reach the innermost stratum and was narrow in span in the plane of the retina (Figs 1*b*, 2).

Serial resectioning of three of the newly identified Golgi-impregnated bipolar cells for electron microscopy demonstrated that those dendritic terminals which reached the level of the cone pedicles, invaginated these structures, and terminated as central elements at cone triads (Fig. 1*c*). Enough sections were recovered from two cells to find that the dendritic terminals occupied the central elements of 8 of 11 and 11 of 15 ribbon synapses respectively. Several of the 'blind' dendrites, those which did not reach the level of cone pedicles in the OPL, were followed to their termination in serial sections. There was no evidence that these processes continued, unimpregnated, to the photoreceptors.

These newly identified bipolar cells sometimes contacted two cones (Fig. 2), as did double-midget bipolar cells, but the two cones contacted by these new bipolar cells were always separated widely by approximately three intercone distances and were never seen to contact two adjacent cones as double-midgets did (Fig. 2). The smaller dendritic cluster of the pair which contacted two cones was often seen to overlap with the large cluster of one which contacted only one cone, and the dendritic clusters of these newly identified bipolar cells were not seen to overlap