primitive features of the embryos (e.g., short snout, circular orbit, and elongated jugal), it is possible that the position of their nares migrated backwards during ontogeny. The extent to which ontogenetic development could have affected the partially to minimally retracted nares of the embryos is uncertain because their position (either partially or fully retracted) remains unclear for most adult titanosaurs (*15*, *16*), but in the newly described *R. krausei*, the external nares are placed on the top of the skull (*5*). The new embryonic evidence contradicts previous ideas coupling narial retraction to quadrate and braincase rostral rotation, which need not have evolved in concert (*16*).

Another notable transformation of the cranial architecture of sauropod dinosaurs is the abbreviation of the infraorbital region characteristic of neosauropods (*6*). In these dinosaurs, the jugal is short and does not contribute to the ventral margin of the skull. It has been suggested (*10*) that the evolution of this apomorphic position of the jugal could have been correlated to the infraorbital shortening experienced by these sauropods. The participation of the jugal in the ventral margin of the new embryonic skulls, whose orbital region is unabbreviated (Fig. 1), is congruent with this suggestion.

The discovery of the new embryonic sauropod skulls provides another example of how developmental data inform our understanding of evolutionary events (*18*). The new ontogenetic evidence suggests that whereas the narial retraction and braincase rotation of the sauropod skull likely evolved independently from each other, the infraorbital abbreviation and the exclusion of the jugal from the ventral margin of the skull could have evolved in concert.

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3. All embryonic remains from Auca Mahuevo belong to the vertebrate paleontology collection (MCF-PVPH) of the Museo Municipal "Carmen Funes" in Plaza Huincul (Province of Neuquén, Argentina).
4. The skull length of the best-preserved specimen (MCF-PVPH-272) is ~35.0 mm from the proximocaudal end of the quadrate to the tip of the rostrum; the horizontal length of its orbit is 13.5 mm. The parietal width, measured from its contribution to the supratemporal fenestra to the interparietal suture, is about 7.6 mm and 8.3 mm in MCF-PVPH-272 and MCF-PVPH-250, respectively. The teeth of the new and previously reported embryos are ~2.0 mm in length (*1*). Estimates based on limb measurements suggest that the total length of the most advanced embryos was ~300 mm (*20*).
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8. Chiappe *et al.*'s (*1*) neosauropod identification of the Auca Mahuevo embryos was primarily based on dental morphology: i.e., the cylindrical shape of the teeth and the absence of denticles in their crowns.
9. Wilson and Sereno (*10*) phylogenetically defined the clade Neosauropoda as the common ancestor of the Late Jurassic diplodocid *Diplodocus longus* and the latest Cretaceous titanosaur *Saltasaurus loricatus* plus all its descendants. These authors also defined the more inclusive clade Eusauropoda as sauropods more closely related to *S. loricatus* than to the Early Jurassic *Vulcanodon karibaensis*.
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Effects of Helpers on Juvenile Development and Survival in Meerkats

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Although breeding success is known to increase with group size in several cooperative mammals, the mechanisms underlying these relationships are uncertain. We show that in wild groups of cooperative meerkats, *Suricata suricatta*, reductions in the ratio of helpers to pups depress the daily weight gain and growth of pups and the daily weight gain of helpers. Increases in the daily weight gain of pups are associated with heavier weights at independence and at 1 year of age, as well as with improved foraging success as juveniles and higher survival rates through the first year of life. These results suggest that the effects of helpers on the fitness of pups extend beyond weaning and that helpers may gain direct as well as indirect benefits by feeding pups.

In social mammals whose young are reared principally by their parents and are rarely (or never) fed directly by other group members, competition for resources commonly increases in large groups, and breeding success either declines with increasing group size or shows no consistent relation to it (*1*, *2*). In contrast, positive relations between breeding success and group size are common in social mammals whose young are reared by helpers (*3*–*8*). Although these correlations suggest that the presence of helpers benefits juveniles in cooperative species, the ecological and behavioral mechanisms underlying them are poorly understood, and group size could affect several different processes that influence juvenile survival, including predation, infanticide, and starvation (*3*).

Like other social mammals whose young receive much of their food from helpers, juvenile survival increases in larger groups of Kalahari meerkats, *Suricata suricatta* (*9*). This cooperative mongoose lives in groups of 2 to 30, consisting of a dominant male and

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female that are the parents of over 80% of young born in the group (*10*) and a variable number of helpers that assist in guarding and feeding young during their first 10 to 12 weeks of life (*11*, *12*). All individuals over 3 months of age assist in feeding pups between the ages of 30 days (when they start to travel with the group) until approximately 90 days (when they forage independently), although the contributions to pup feeding of juveniles 3 to 6 months old are often small.

Across litters, both the amount of food that pups receive (Fig. 1A) and their rate of daily weight gain (Fig. 1B) (*13*) rise with the ratio of helpers to pups, which increases with group size (*14*). These correlations could, however, be a consequence of independent effects of territory quality on food intake rate, pup weight gain, and number of helpers (*15*). To determine whether the presence of helpers exerts a causal effect on juvenile development, studies of cooperative birds have removed a proportion of helpers (*15*, *16*). However, because manipulations of this kind may disrupt social relationships within the group, potentially affecting contributions to cooperative activities (*16*), we preferred to manipulate the ratio of helpers to pups by temporarily removing pups from or adding pups to litters (*17*). Our experiments show that increases in helper:pup ratios raise the rate of weight gain in pups (Fig. 2A), whereas reductions lower their rate of weight gain (Fig. 2B). Helpers fed introduced pups as frequently as the group's own pups (*18*), and reductions in helper:pup ratios also reduced the daily weight gain of helpers (Fig. 2D). Helpers feeding experimentally enlarged litters were probably responding to an increased frequency of begging calls given by unsatisfied pups, because hungry pups call more frequently and playbacks of pup begging calls raise the proportion of food items given to pups (*19*). In contrast, increases in helper:pup ratios did not lead to a significant increase in the rate of weight gain of helpers, though there was a nonsignificant trend in this direction (Fig. 2C).

High rates of daily weight gain have beneficial consequences for the subsequent development of pups. Average rates of daily weight gain during peak provisioning (between 35 and 75 days after birth) are correlated with body weight at independence (3 to 4 months) (Fig. 1C) as well as at adulthood (12 to 13 months) (Fig. 1D) (*20*). These effects were confirmed by experimentally feeding pups (*21*): Individual pups that were fed with 12 g of egg twice per day during the period of pup feeding showed an average daily (12-hour) weight gain that was 7 g higher than that of unfed controls ($F_{1,19}$ = 11.40, P = 0.003) and were heavier as juveniles, subadults, and adults (at 3 to 4 months, $F_{1,20}$ = 5.29, P = 0.032; at 6 to 7 months, $F_{1,14}$ = 6.34, P = 0.025; at 12 to 13 months, $F_{1,6}$ = 9.42, P = 0.022). Pups that are relatively heavy at independence catch more food items (Fig. 1E) and show higher rates of daily weight gain (Fig. 1F). Finally, the rate of daily weight gain of pups during peak provisioning was consistently related to their survival between emergence and 12 months (Table 1). After daily weight gain is included, helper:pup ratios have no additional effect on pup survival, because their effects are absorbed by the inclusion of daily weight gain in the model. However, pup survival increases with group size when other effects are controlled for, possibly because the effectiveness of predator detection rises in large groups (*9*).

Our results show that the presence of

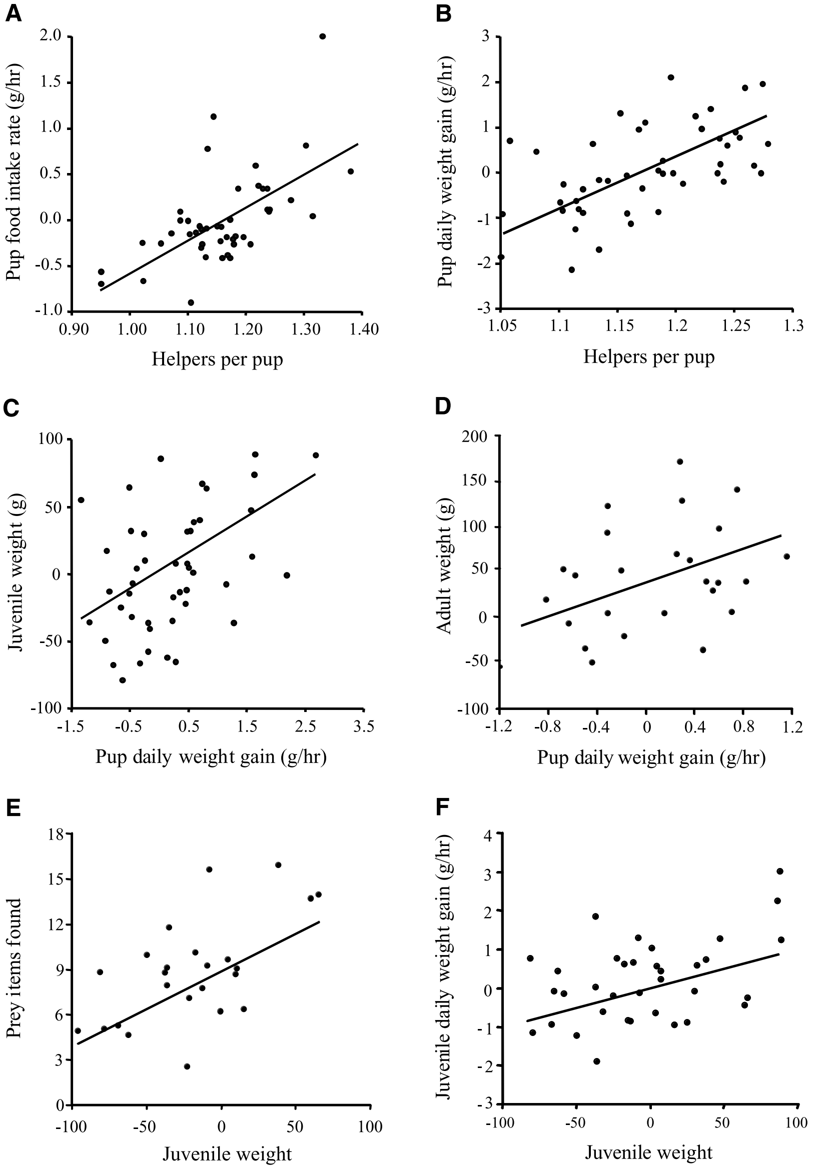

Fig. 1. Downstream effects of pup feeding by helpers on the daily weight gain of pups, their weight and foraging success at independence, and their weight at adulthood (*13*, *14*, *20*). Analyses were conducted on means for 46 litters [(A) through (C)], 26 litters [(D) through (E)], and 35 litters (F) and controlled for the effects of repeated measures within eight groups. Axes with negative values depict residual values obtained from regressions of the variable in question on age. (**A**) Correlation between helper:pup ratios and mean rate of estimated food intake by individual pups between 35 and 75 days old, measured in grams per hour ($F_{1,37}$ = 21.31, $P < 0.001$). (**B**) Correlation between helper:pup ratios and mean daily weight gain of pups between 35 and 75 days old ($F_{1,37}$ = 12.74, P = 0.001). (**C**) Correlation between mean daily weight gain of pups between 35 and 75 days old and mean body weight of the same individuals at independence (3 to 4 months) ($F_{1,37}$ = 10.83, P = 0.002). (**D**) Correlation between mean daily weight gain of pups between 35 and 75 days old and mean body weight of the same individuals at adulthood (12 to 13 months) ($F_{1,17}$ = 5.73, P = 0.041). (**E**) Correlation between the weight of individuals at independence and the number of food items they find per hour at independence ($F_{1,17}$ = 8.6, P = 0.01). (**F**) Correlation between the body weight of pups at independence, after pup feeding by helpers had ceased, and their mean residual daily weight gain over the same period ($F_{1,26}$ = 7.29, P = 0.012).

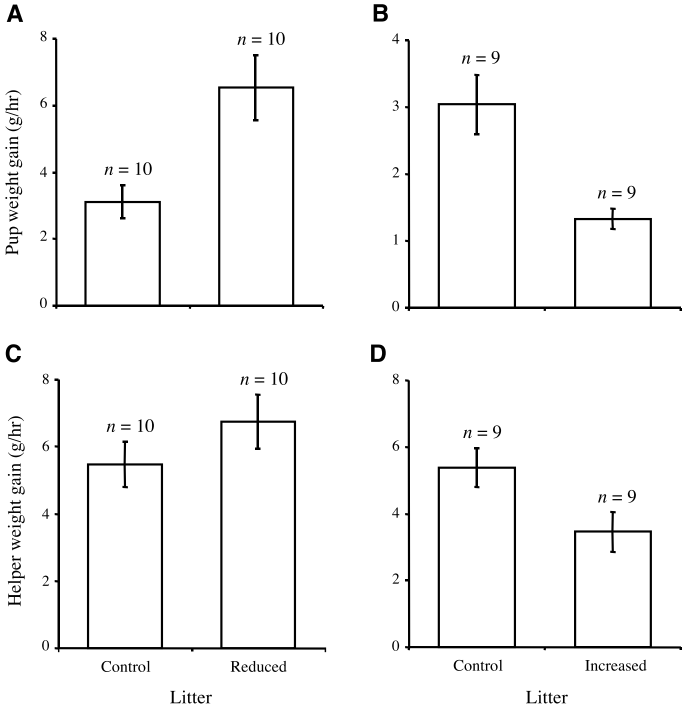

Fig. 2. Effects of manipulating helper:pup ratios (*17*) on daily weight gain of pups and helpers. In this experiment, helper:pup ratios were either temporarily increased by removing 75% of pups or were reduced by increasing litter size by 75%. Control values were mean measures of daily weight gain in pups and helpers in the same group within 2 days of the experiment. Analyses used paired *t* tests and one-tailed *P* values are shown. *n*, number of temporary removals. (**A**) Pups in reduced litters (high helper:pup ratios) showed a 100% increase in their daily weight gain ($t_9 = 3.86$, $P < 0.003$) as well as in the number of items they received per hour ($t_9 = 4.71$, $P < 0.001$). (**B**) Pups in increased litters (low helper:pup ratios) showed a 45% reduction in their daily weight gain ($t_8 = 3.65$, $P < 0.004$) as well as a 34% reduction in items received per hour ($t_8 = 2.81$, $P < 0.02$). Resident pups in increased litters showed a 38% decrease in daily weight gain ($t_8 = 2.22$, $P < 0.02$) as well as a 32% reduction in items received per hour ($t_8 = 1.57$, $P = 0.077$). (**C**) Helpers feeding reduced litters showed a nonsignificant tendency for daily weight gain to increase as compared with values for the same individuals on the four previous days ($t_9 = -1.24$, $P = 0.12$). (**D**) Helpers feeding increased litters showed a significant reduction in their daily weight gain of 31% as compared with values for the same individuals on the four previous days ($t_8 = 3.41$, $P < 0.005$).

Table 1. Generalized linear mixed model of the factors associated with individual survival from burrow emergence (at approximately 18 days) to 1 year. Analysis was conducted on 135 individuals from 41 litters in eight groups using the program GENSTAT 5.4.1 (*30*). The data were fitted to a binomial error structure with logit-link function, and litter identity was fitted as a random term to control for repeated measures within litters (*1*–*6*). Probability of survival to 1 year was positively influenced by average group size between death or 1 year (whichever was soonest) and mean age-related weight gain during the peak pup provisioning period, although survivorship declined again in large groups. Daily weight gain was the hourly weight gain of pups during the morning feeding period between the ages of 35 and 75 days (or death). Individuals were only included in the model if they were born a year or more before the end of data collection.

Model terms	Wald statistic	d.f.	*P*
Group size	9.32	2	0.009
Daily weight gain (g/hour)	4.38	1	0.036
Sex	2.82	1	0.093
Emergence weight	0.62	1	0.43
Helper:pup ratio	0.51	1	0.48
Dominance status of mother	0.04	1	0.85

Minimal model	Average effect	SE
Constant	0.91	0.47
Group size		
<12	0	
12–19	1.36	0.63–0.66
>19	−0.52	
Daily weight gain (g/hour)	0.022	0.0094

helpers has substantial benefits for the daily weight gain, growth, and survival of meerkat pups. In small groups with low helper:pup ratios, helpers do not provide sufficient food to allow pups to maximize their growth rates, leading to reductions in their body weight and survival over the first year of life. The effects of helpers on early development and subsequent survival in meerkats and some other cooperative breeders (*22*) parallel the associations between maternal characteristics, early development, and adult fitness found in many other vertebrates (*23*). These results show that estimates of the effects of helpers on the survival of young to fledging or weaning are likely to underestimate the extent to which helpers affect the fitness of developing pups. Moreover, in addition to any indirect benefits gained by helpers assisting kin (*24*), these effects are likely to contribute to the direct fitness of the helpers themselves if foraging success or survival increase with group size (*9*, *10*, *25*, *26*) or if the number or condition of pups raised reduces the efforts that individual helpers need to devote to raising subsequent litters (*27*, *28*).

The contrasting relations between group size and breeding success found in social mammals whose young are fed by parents alone (*1*, *2*) and those whose young are fed by parents and helpers (*3*–*8*) suggest that strong positive correlations between group size and breeding success may be confined to species, such as meerkats, in which young obtain much of their food from helpers or are dependent on them for some other resource. In contrast, when dependent young obtain most of their food from parents and little from helpers, the negative effects of increased group size on resource competition may offset the beneficial consequences of helpers, so that breeding success is unrelated or even negatively related to group size (*29*).

Differences in the extent to which breeding success and juvenile survival depend on group size have important implications for the population dynamics of social species (*4*, *7*). Where members of small groups show reduced survival and reproductive success, density-independent factors that reduce survival, local density, and group size may depress average breeding success and raise the frequency of group extinctions. The magnitude of these "Allee" effects (inverse density dependence) is likely to increase with the dependence of breeding success and survival on group size (*4*) and, as expected, recent studies of several cooperative breeders have revealed high rates of group extinction (*4*, *26*).

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14. Group size was the mean number of individuals over 3 months old in the group over the relevant period. Helper:pup ratios were the ratios of individuals over 3 months old (excluding the dominant male and female) to pups under 3 months old. Because there was no association between group size and the average size of litters born to dominants at emergence [general linear model (GLM) of 77 litters, controlling for the effects of mother identity, $F_{1,58} = 2.86$, $P = 0.096$], the ratio of helpers to pups increased in larger groups (GLM of 77 litters, controlling for group identity, $F_{1,62} = 34.29$, $P < 0.001$).
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18. Pups that were accepted by their temporary foster groups were fed as frequently by group members as were the group's own pups [paired *t* test (t_8) = –1.52, $P = 0.17$), although the morning weight gain of introduced pups was lower than that of the group's own pups ($t_8 = –2.61$, $P = 0.03$). Pups and all other group members were weighed at the beginning and end of the introduction with the use of standard techniques, and these weights were used to calculate weight gains per hour (*P* values here are two-tailed because there was no basis for predicting the outcome of these tests in advance).
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21. For pup feeding experiments, in 11 litters with an average size of 3.4 pups per litter, we randomly assigned half the pups in each litter to an experimental group and fed each of these pups with about 12 g of hard-boiled egg at the end of morning and evening activity periods. The other pups in the litter received no additional food. Sample sizes in these analyses were the number of fed and unfed pups, and tests shown are based on GLMs controlling for sex and repeated measures within litters. Pup feeding was maintained until the animals were 60 days old, and the frequency with which they were fed by helpers had started to fall (*27*).
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Loss of Caveolae, Vascular Dysfunction, and Pulmonary Defects in Caveolin-1 Gene-Disrupted Mice

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Caveolae are plasma membrane invaginations that may play an important role in numerous cellular processes including transport, signaling, and tumor suppression. By targeted disruption of caveolin-1, the main protein component of caveolae, we generated mice that lacked caveolae. The absence of this organelle impaired nitric oxide and calcium signaling in the cardiovascular system, causing aberrations in endothelium-dependent relaxation, contractility, and maintenance of myogenic tone. In addition, the lungs of knockout animals displayed thickening of alveolar septa caused by uncontrolled endothelial cell proliferation and fibrosis, resulting in severe physical limitations in caveolin-1–disrupted mice. Thus, caveolin-1 and caveolae play a fundamental role in organizing multiple signaling pathways in the cell.

Caveolae are characteristic flask-shaped invaginations of the plasma membrane with a diameter of 50 to 100 nm. They are present on many cell types, including endothelial cells, smooth muscle cells, and adipocytes (*1*, *2*). Fifty years after the discovery of caveolae (*3*), their function is still controversial and may include transcytosis of solutes through endothelial cells (*4*), cholesterol transport (*5*), potocytosis (*6*), signal transduction (*2*, *7*), and tumor suppression (*8*). VIP21/caveolin-1 (cav-1), a protein of 21 to 22 kD, is so far the best biochemical marker for caveolae (*9*, *10*). This integral membrane protein is a member of the caveolin-gene family, binds cholesterol (*11*), and forms high molecular weight oligomers (*12*).

To address the role of cav-1 on caveolae formation and its effect on signal transduction, we generated mice lacking the cav-1 gene by excision of exon-3 (Fig. 1A) (*13*). This encodes the transmembrane domain, the palmitoylation sites, and the so-called

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