would complement those of somatostatin, thereby providing the means for both short- and long-term inhibition of GH secretion.

We have described the in vitro stimulatory effects of SM-C on hypothalamic somatostatin release and inhibitory effects on pituitary GH secretion. Together with our previous report that GH directly stimulates hypothalamic somatostatin accumulation and release, our studies provide a more complete picture of pituitary GH regulation: GH promotes synthesis and release of the somatomedins, including SM-C. Both SM-C and GH act rapidly at the level of the hypothalamus (primarily the MBH) to stimulate somatostatin release, thereby inhibiting further GH secretion. The possibility of a simultaneous effect of SM-C or GH on hypothalamic GH-releasing factor cannot as yet be determined. More prolonged exposure to SM-C causes direct inhibition of GH release by the pituitary and could account for some of the impaired GH responses seen in patients with GH-secreting pituitary tumors.

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8. Sprague-Dawley rats housed under a 14:10 light-dark cycle and constant temperature (20°C) were decapitated with minimum handling and stress. The brain was rapidly (< 2 minutes) removed to an ice-cold surface. The MBH (defined by the lateral hypothalamic sulci, the mammillary bodies, and the optic chiasm) was removed with curved-bladed scissors to a depth of 2 mm (weight, 22 ± 3 mg; $N = 10$). A cut made in the frontal plane at the level of the optic chiasm and a parallel cut 3 mm rostral to the first yielded a slice of brain from which SPO could be defined (dorsally by the corpus callosum, laterally by vertical lines through the lateral ventricles, and ventrally by the base of the brain) and removed (weight, 36 ± 4 mg; $N = 10$).
9. Highly purified SM-C was prepared by the method of J. M. Horner, F. Liu, and R. L. Hintz [*J. Clin. Endocrinol. Metab.* **47**, 1287 (1978)] and shown to be homogenous by gel electrophoresis and thin-layer isoelectric focusing. This preparation is identical to IGF-1 and the SM-C preparation of J. J. Van Wyk in several different radioligand assays [*ibid.* **50**, 405 (1980)].
10. Bovine serum albumin provided a control for nonspecific protein effects; proinsulin has a structure similar to that of IGF-1 and -2 (though possibly not to that of SM-C); insulin shares many biologic effects with the somatomedins (though of a lesser potency); and epidermal growth factor represents a non-GH-dependent factor with anabolic and trophic effects on tissue.
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18. Supported by NIH grants AM 18722 and AM 24085. Eli Lilly and Co., Indianapolis, Ind., provided the porcine proinsulin and insulin, and S. Cohen provided the epidermal growth factor. The pituitary hormone distribution program of the National Institute of Arthritis, Metabolism, and Digestive Diseases provided the materials used in the rat GH and rat prolactin radioimmunoassays.

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Infant Carrying by Male Chacma Baboons

Abstract. *Male chacma baboons,* Papio ursinus, *carry their offspring during confrontations with higher ranking immigrant males, who are a threat to the infants' lives. The infants sometimes initiate these confrontations by approaching and provoking immigrant males when protective males are close by. Mothers rarely interfere during these interactions.*

A frequently observed but poorly understood feature of savanna baboon (*Papio* spp.) societies is that an adult male sometimes carries an infant during interactions with another male (*1–3*). Explanations of this behavior, originally termed agonistic buffering (*4*), are that by carrying an infant a male reduces his probability of being attacked (*1–3*) or increases his probability of gaining access to an estrous female (*2*) or food (*2*, *3*). The assumption is that the carrying male gains an advantage by exploiting an infant who is probably the opponent's offspring (*2*). In this report we present the opposite interpretation: that the infant is probably the carrying male's offspring and that carrying protects the infant from potentially infanticidal immigrants. Thus, we identify infant carrying as a form of paternal care. This interpretation provides a new link in the understanding of paternal investment (*5*) and infanticide (*6*) in polygamous primate groups.

During a 3-year study of chacma baboons (*Papio ursinus*) in the Moremi Wildlife Reserve, Botswana, we saw adult males kill only two infants and wound two others (*7*). Three of the attackers were immigrant males; the fourth was unidentified. [Male baboons have also attacked infants at other study sites (*3*, *6*, *8*).] Infanticide may be infrequent because resident troop members protect infants from immigrant males (*6*, *9*).

Our analysis of infant carrying by males focuses on the infant's paternity. Males compete to mate with females, and dominant males sire most of the infants in a troop (*10*). This conclusion is based on field observations of mating patterns 3 days before the female's estrous swelling begins deflating ("D − 3"). Studies of reproduction in captive baboons suggest that matings on D − 3 have the highest probability of resulting in conception (*11*). Another factor influencing paternity is that males leave one troop and join another at least once in their lifetimes (*9*): a male joining a troop after an infant's conception cannot be the father.

The effect of infant death on a mother's reproductive behavior (*12*) is another important aspect in this analysis. Baboon infants are weaned at about 12 months of age, and mothers conceive 18 months (532 ± 23 days, $N = 13$) after the birth of an infant who survives to weaning. However, if an infant dies before weaning, the mother becomes sexually receptive after a few weeks and conceives 4 months (134 ± 19 days, $N = 8$) after the death. Thus, by killing an unweaned infant, a male enhances his opportunity to impregnate the mother earlier than he could otherwise (*6*, *13*).

Table 1. Mean relative social rank of males when they carried an infant during an interaction with a male opponent and when the infant was conceived. Relative social rank is the fraction of other adult male group members who are subordinate to a given individual. N.A., not applicable.

Male	Number of times male carried an infant	Mean relative social rank	
		At conception	At interaction
WCK	47	0.98	0.81
WCF	7	0.97	0.00
WBH	5	0.90	0.38
WJO	2	0.12	0.20
CSH	18	0.65	0.14
CJT	13	0.72	0.87
CRK	11	0.74	0.00
CZL	5	1.00	0.22
CBS	3	0.92	0.30
CTP*	1	N.A.	0.44

*Absent at the time of conception of the carried infant.

Top-ranking, or alpha, immigrant males may benefit most from killing infants because they have the highest probability of subsequently impregnating the mother. The median tenure of males at alpha rank is 5 months (range, 1 to 12 months, $N = 9$). By killing an infant, an alpha male substantially increases the probability that when the mother becomes sexually receptive again he will still be alpha.

We observed two chacma baboon troops in Moremi between September 1979 and June 1980 and recorded 112 interactions in which infants were carried. The troops were designated C and W and averaged 70 and 72 members, including nine and six adult males, respectively. The average number of interactions per observation hour per troop was 0.4. The median duration of these interactions was 10 seconds (range, 1 to > 360 seconds). One interaction escalated into a fight, with canine fencing between the males, but there were no injuries during any interaction (*3*).

Evidence that males carried their own offspring is as follows: (i) nine of ten carrying males were troop members when the carried infant was conceived, and these males carried infants in all but one of the 112 interactions (Table 1) (*3*); (ii) the nine males had had significantly higher than average social rank when the infants they carried were conceived ($P < .05$, sign test, $N = 9$); and (iii) we identified the probable father (based on D − 3 observations) of ten of the 25 infants carried. All of these males subsequently carried their probable offspring during interactions with other males.

The opposite pattern prevailed for the opponents of carrying males. Nine of the 12 opponents observed immigrated after the carried infant's conception (Table 2) (*1, 3*). Of the 112 interactions, three involved opponents who were troop members at the time of the infant's conception. Two of these opponents, WSM and CJT, were low-ranking subadults at the time of conception and unlikely to be fathers. Thus, all the opponents, whether present or absent at conception of the carried infants, were probably not the fathers.

In 28 of 29 carrying male–opponent combinations, the opponent was dominant to the carrying male ($P < .001$, sign test) (*14*). Carrying males held high rank at the time of an infant's conception, but had dropped significantly in rank by the time they carried the infant ($P < .05$, Wilcoxon signed-ranks test, $N = 9$). Opponents were high-ranking nonfathers (Table 2), that is, were most likely to benefit from killing the infants. These results support the interpretation that carrying males are protecting their own offspring rather than exploiting unrelated infants.

Why should carrying an infant be an effective means of protecting it against a dominant male? We suggest that infant carrying communicates the willingness of fathers to protect their progeny regardless of the opponent's rank. In these confrontations the payoff to the carrying male, the continued survival of an offspring, is greater than the payoff to the opponent, a higher probability of siring an infant in the future.

Other features support our interpretation. (i) Unweaned infants less than a year old were carried in 101 of 112 interactions (*1, 3*). Unweaned infants may be at the greatest risk of attack by immigrant males (*13*). (ii) In 13 interactions the infants elicited protective carrying by approaching and threatening immigrant males (*3*). In 18 interactions the infants initiated contact with protective males and in 12 interactions the latter initiated contact. (iii) Baboon mothers rarely interfere with males who carry their infants, and are constant associates of these males (*8*). In only one interaction did a mother attempt to retrieve her infant before the interaction ended. Females observe the interactions from a distance, usually 5 m or more, and are available to retrieve infants when the interactions are completed. (iv) Mothers carrying unweaned infants show alarm by raising their tails when in close proximity to immigrant males (*15*). Sometimes they scream when closely approached by immigrants (*9*), which may attract protective males. This antagonism by mothers and infants toward immigrants suggests that these males are a threat to the lives of the infants.

Table 2. Mean relative social rank of opponents at the time of interaction with a male carrying an infant and at the time the infant was conceived. N.A., not applicable.

Male	Present at conception	Number of times male was opponent	Mean relative social rank	
			At conception	At interaction
WBH	Yes	1	0.56	0.40
WSM	Yes	1	0.00	0.80
CJT	Yes	1	0.00	1.00
WNR	No	57	N.A.	1.00
WCK	No	2	N.A.	0.80
CBB	No	19	N.A.	0.91
CMD	No	11	N.A.	0.92
CPD	No	7	N.A.	0.93
CBR	No	5	N.A.	0.33
CSK	No	4	N.A.	0.67
CPG	No	2	N.A.	0.95
CTP	No	2	N.A.	0.64

Contests over food resources or estrous females were not a general feature of infant carrying in our population. Opponents were in consort with estrous females during nine interactions, and carrying males never gained access to these females. Also, carrying males sometimes spatially displaced their opponents (*16*), but only once gained access to food. These results further support rejection of the infant exploitation hypothesis.

In a recent study of infant carrying by male baboons (*P. anubis*) at Gombe, Tanzania, Packer (*3*) concluded that alternative explanations of this behavior are needed. Observations at Gombe (*1, 3*) are consistent with our interpretation, which thus may also apply to other savanna baboon populations.

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7. An immigrant killed a 4-day-old infant immediately after the mother was tranquilized during physiological studies. This event was completely unanticipated because previous studies gave no suggestion that infanticide was a feature of savanna baboon societies. Three other attacks occurred under unmodified conditions. An unidentified male killed an unweaned 9-month-old

infant. An immigrant male bit an 11-month-old infant behind the ear (K. S. Smith, personal communication). Finally, a male from an unknown troop wounded a weaned 14-month-old juvenile during an intertroop interaction.
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16. Carrying males chased or displaced opponents during four interactions and were chased or displaced by opponents during 11 interactions.
17. We are indebted to Mr. Ngwamotsoko and the Office of the President of Botswana for permission to study in Botswana. We thank K. S. Smith for invaluable help in the field and P. S. Rodman, R. L. Tilson, L. R. Becker, S. Blaffer Hrdy, R. Boyd, A. B. Clark, R. O. Davis, M. F. Miller, D. Owens, M. Owens, M. P. Rowe, J. B. Silk, and D. M. Stein for comments on the manuscript. Supported by NIH grant 5-RO1-RR01078.

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Vagotomy Abolishes Cues of Satiety Produced by Gastric Distension

Abstract. *Subdiaphragmatic vagotomy in the rat abolishes responsiveness to gastric distension, one of the cues of satiety. However, vagotomized rats remain responsive to gastric nutrient content, another cue of satiety.*

Meal size in the rat is regulated by sensory information originating from the preintestinal segment of the gastrointestinal tract. When passage of food from the stomach to the intestine is prevented by blocking the pyloric sphincter with a noose (*1, 2*) or an inflatable cuff (*3, 4*), subjects consume meals of normal size. Since rats overeat when food is removed from their stomachs (*2–5*), gastric rather than oropharyngeal receptors are the likely source of satiety messages.

The stomach produces two types of satiety signals. One conveys information concerning the nutrient content of the stomach and is independent of gastric volume. The other signals gastric distension and is given only after the animal has consumed a large meal (*4*). We examined the effects of interrupting the parasympathetic innervation of the stomach on these satiety signals and demonstrated the pathway of one of them to the central nervous system.

Nine male Sprague-Dawley rats (325 to 495 g) were used as subjects. The animals were habituated to a restricted feeding schedule consisting of two meals of undiluted canned milk (Carnation) a day. The first meal (30 minutes) began at 1000 hours while the subjects were in restraining cages. The second meal (3 hours) began at 1600 hours in the home cages. The animals had free access to water at all times, except when undergoing testing in the restraining cages.

After the food intakes and weights of the subjects had stabilized, they were randomly assigned to a vagotomized or a control group. Six subjects were vagotomized at the subdiaphragmatic level by stripping all neural and connective tissue surrounding the 3- to 5-mm portion of the esophagus immediately rostral to the stomach (*6*). The hepatic branch of the nerve was spared. In three control subjects the subdiaphragmatic vagus was identified but not injured.

All subjects were allowed to recover for 21 days under the feeding conditions described. They were then implanted with inflatable pyloric cuffs and stomach tubes (*7*). After a second convalescence period of at least 10 days, the ingestive behavior of the subjects during their 30-minute meals was examined. The measurements consisted of (i) baseline consumption, (ii) consumption when a proportionate amount (50 percent by volume) of 0.9 percent saline was infused into the rat's stomach as it drank (*8*), and (iii) consumption when a fixed volume (5 ml) was siphoned from the rat's stomach as it drank at the beginning of the test. These measurements were made in the order described, first with the pylorus unoccluded, then with pyloric cuff inflated with 1.5 ml of water to prevent emptying of the stomach. The results were analyzed with one-tailed *t*-tests for paired data.

Figure 1 presents a summary of the results. After being infused with saline, the control rats decreased their intake of milk by 23 and 22 percent after 15 and 30 minutes, respectively ($t = 4.529$, $P < .05$ and $t = 4.695$, $P < .05$, respectively). The vagotomized subjects showed a small but nonsignificant increase in consumption (7 and 5 percent). When 5 ml was siphoned from the stomachs of the control rats, they increased their intake by 6.2 and 3.5 ml after 15 and 30 minutes, respectively. The increase measured after 15 minutes is significant ($t = 15.105$, $P < .01$); the increase measured after 30 minutes is not. Vagotomized rats drank 6.5 and 7.1 ml more when 5 ml was siphoned from their stomachs; both increases are significant at $P < .01$ ($t = 3.758$ and 4.369, respectively). The same pattern of results was observed when the subjects were tested after their pyloric cuffs were inflated to confine the milk to their stomachs.

Since the vagotomized subjects drank considerably less than the controls, their milk intake was measured when a larger (100 percent) volume of saline was infused into their stomachs as they drank, thus doubling intragastric volume. Once again, these subjects were insensitive to the increase in volume. Their intakes after 15 and 30 minutes were 9.7 and 10.7 ml in the control condition and 10.7 and 11.1 ml in the saline infusion condition

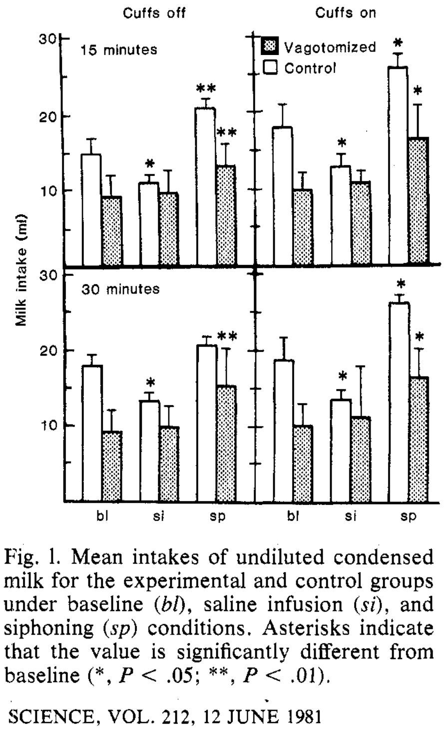

Fig. 1. Mean intakes of undiluted condensed milk for the experimental and control groups under baseline (*bl*), saline infusion (*si*), and siphoning (*sp*) conditions. Asterisks indicate that the value is significantly different from baseline (*, $P < .05$; **, $P < .01$).

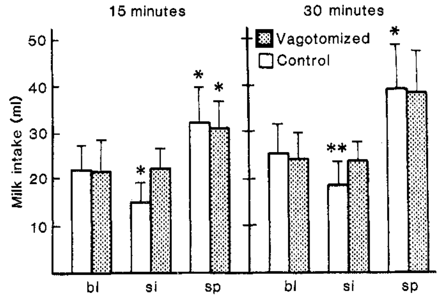

Fig. 2. Mean intakes of diluted milk for the experimental and control groups under baseline, saline infusion, and siphoning conditions. Abbreviations are as in Fig. 1.