covered at the site. One (Fig. 4b) was found eroding out of the old arroyo deposits and is much larger than the one recovered under the bone pile. Two others were recovered with mammoth bone but in what are believed to be slump deposits that fell into the old arroyo from the banks and were subsequently covered with alluvium. This suggests that much of the human activities occurred outside the old arroyo. One of the latter projectile points (Fig. 4a) is similar in shape but larger than the one from under the bone pile while the other is similar in shape and in size. All projectile points were made of local flaking stone available in the Bighorn Mountains. They are also somewhat different typologically from the Clovis projectile points recovered in other sites where mammoths have been associated with human activities (*1, 3, 4*).

Several interpretations are possible concerning the placement of the projectile point under the mammoth pelvis. The projectile point may have been lost during normal site activities and bones just happened to have been piled on top of it. On the other hand, it may have been lodged in the tissues of the bones that were stacked. Another possibility is that it was an offering deliberately placed at the bottom of the bone pile. While speculation of this nature can be continued indefinitely, the presence of the projectile point along with the other artifacts leaves no doubt of the human involvement in the placement of the bone pile.

There is little, if any, evidence of the techniques used for killing, butchering, and processing the mammoths at the Colby site. The bones are too deteriorated to retain cutting and chopping marks, although some may have been deliberately broken. The artifacts found in the area are not commensurate with the requirements for butchering many large animals. Also, large numbers of flakes from tool-sharpening, which might be expected at a site used for mammoth butchering and processing, are not present, suggesting the possibility that mammoths were not cut up in the same way as bison (*7–10*). However, it is postulated that the main human activities occurred outside the old arroyo bottom, and that the areas where these activities occurred have since been eroded downward several meters and moved downstream.

The stacking could have occurred as the bones were stripped of flesh or it could have occurred months or even a year or so later. Bone stacking was common in Paleo-Indian bison kills (*10, 12*), so the same practice in mammoth sites is not surprising. Whether it represents human activity of little consequence or something with deeper cultural significance is unknown. In conclusion, the mammoth bone piles in the old arroyo at the Colby site are believed to have resulted from activities that were only indirectly related to the butchering of the animals and the processing of the meat, although they might have been placed there to protect freshly killed meat from carnivores.

G. C. FRISON

Department of Anthropology,
University of Wyoming, Laramie 82070

References and Notes

1. H. M. Wormington, "Ancient man in North America," *Denver Mus. Nat. Hist. Publ.* (1957).
2. J. D. Figgins, *Proc. Colo. Mus. Nat. Hist. 12* (1933); F. C. Leonhardy, Ed., "Domebo, a Paleo-Indian mammoth kill in the prairie-plains," *Contrib. No. 1, Mus. Great Plains Lawton* (1966); E. W. Haury, E. B. Sayles, W. W. Wasley, *Am. Antiq.* **25**, 2 (1959); E. W. Haury, *ibid.* **19**, 1 (1953); E. T. Hemmings and C. V. Haynes, *J. Ariz. Acad. Sci.* **5**, 3 (1969); C. V. Haynes, *Science* **166**, 709 (1969).
3. J. J. Hester, "Blackwater locality No. 1," *Fort Burgwin Res. Center Publ. No. 8* (1972).
4. C. V. Haynes, *Science* **145**, 1408 (1964).
5. J. B. Wheat, *Arct. Anthropol.* **8**, 2 (1971); C. V. Haynes, *Sci. Am.* **214**, 104 (June 1966).
6. C. A. Reher, in *The Casper Site, a Hell Gap Bison Kill on the High Plains*, G. C. Frison, Ed. (Academic Press, New York, 1974).
7. G. C. Frison, M. Wilson, D. Wilson, *Am. Antiq.* **41**, 1 (1976).
8. J. P. Albanese, paper presented at 33rd Plains Conference, Lincoln, Neb., 1975.
9. C. Madden, in preparation.
10. G. C. Frison, in *The Caster Site, a Hell Gap Bison Kill on the High Plains*, G. C. Frison, Ed. (Academic Press, New York, 1974).
11. ——— and M. Wilson, *Guidebook* (Wyoming Geological Association, Casper, 1975).
12. J. B. Wheat, *Soc. Am. Archeol. Mem. 26* (1972).
13. I thank the National Science Foundation, University of Wyoming, and Wyoming Recreation Commission for research support, and also the William Perry and Kenneth Barger families for access to the Colby site. J. Albanese performed geologic mapping of the site area.

2 June 1976; revised 10 August 1976

Sex-Specific Cannibalism in the Rotifer *Asplanchna sieboldi*

Abstract. *In one clone, large-morphotype females rarely exhibit tactile feeding responses to their ingestible, male clonemates but readily attack small-morphotype female clonemates and males of another, taxonomically distinct, clone. In the latter clone, cannibal females lack such selectivity, but their males are well protected from capture by very large, lateral body-wall outgrowths.*

Asplanchna sieboldi is a predatory, planktonic rotifer which reproduces either by female parthenogenesis or bisexually. Females are trimorphic, and morphotype transformations require two or more parthenogenetic generations. The relatively small (550 to 700 μm) saccate females produce larger (800 to 1200 μm) cruciform females only when the diet contains tocopherol (vitamin E) (*1*). Cruciforms have four protrusible, more or less pronounced, body-wall outgrowths and may produce even larger (800 to 1700 μm) bell-shaped or campanulate females when the diet contains tocopherol as well as congeneric or other large prey (*2, 3*). Cruciforms and especially campanulates are cannibalistic (*2–4*).

Males, which are characteristically produced by certain (mictic) cruciform females (*3*), are relatively small (400 to 850 μm) and lack food-capturing and digestive systems (Fig. 1). They regularly co-occur with cruciform and campanulate females (*3, 5, 6*) and thus are susceptible to cannibalism, perhaps especially when the male moves around the surface of the female during mating. However, males, just like cruciform females, have extensible, lateral body-wall outgrowths which can effectively protect them from capture by attacking conspecifics and which almost certainly evolved in response to cannibalism (*5*). The study reported here shows that males of at least one clone are protected by another mechanism: they do not elicit tactile feeding responses in cannibalistic, female clonemates.

Saccate, cruciform, and campanulate females from the taxonomically distinct clones B and C (*7*) were maintained at 26°C (*3, 4*). Males of both clones were obtained by inducing saccate-to-cruciform transformations with tocopherol-containing diets (*8*). Cruciform and campanulate predators were starved for 2 to 6 hours before an experiment and then placed singly in 1-ml-capacity depressions with prey. Male and female prey were tested together in one depression; male prey from the two clones were tested in separate depressions. Each predator was responsive, made at least several contacts with both prey types, and was removed once it ingested a prey item. Predators were observed continuously at a magnification of 18 diameters with a stereomicroscope. The predators, which appear to swim randomly, may or may not respond to contact with a potential prey. Responses seem to be mediated by cephalic contact chemoreceptors (*4*). A response involves directed movements of the head, usually accompanied by open-

Table 1. Tactile feeding responses of campanulate (Ca) and cruciform (Cr) predators of the rotifer *Asplanchna sieboldi* to male (M) and saccate female (F) prey of the same and different clones.

Set of experiments	Prey		Predator			Predator response			P
	Clone	Sex	Clone	Morphotype	Number	No response	Response	Total contacts	
1	B	F	B	Ca	27	13	64	77	$< 1 \times 10^{-9}$
	B	M				117	23	140	
2	B	M	B	Ca	57	477	11	488	$< 1 \times 10^{-9}$
	C	M				107	364	471	
3	C	M	C	Cr	35	163	167	330	8.2×10^{-2}
	B	M				104	143	247	
4	C	M	C	Ca	11	11	49	60	

ing of the mouth and working of the jaws. Predators may regularly respond to prey which, because of their shape or large size, cannot be captured in the pharynx and swallowed. Prey size itself, at least within a range of 300 to 800 μm, does not seem to affect response initiation (*4*). Females exhibit no mating behavior when in the presence of or in contact with males, and so all predator responses observed were clearly feeding responses. Proportions of predator contacts resulting in responses were compared by using row-by-column tests of independence and the *G*-statistic (*9*). Probabilities for *G*-values were calculated from the chi-square distribution by using a program (*10*) for the HP-65 calculator.

The results of four sets of experiments are summarized in Table 1. In the first set, clone B campanulate predators (~ 850 μm) readily responded to and attacked saccate clonemates, as previously reported (*4*), but only rarely reacted to similarly sized male clonemates (~ 530 μm). In the second set of experiments, these campanulates responded even less frequently to male clonemates but usually did attack males of clone C (~ 750 μm). In contrast, the third and fourth sets of experiments show that clone C cruciform (~ 1000 μm) and campanulate (~ 1500 μm) predators exhibited little or no selectivity and readily responded to and attacked male clonemates. There was some tendency for the clone C cruciforms to react less often to males of their own clone than those of clone B, but the difference was not significant. Clone C campanulates were more voracious than cruciforms and vigorously attacked male clonemates; only two of them did not respond to all contacts, and one of these accounted for 10 of the 11 exceptions.

Clearly, clone B males are efficiently protected against predation from campanulate clonemates. They do not elicit feeding responses in these cannibals, and so they are not subjected to attacks by them. Clone C males are not free from the predatory behavior of cannibal clonemates. They are, however, protected from capture by their size and, especially, their prominent body-wall outgrowths (Fig. 1). The mean body length (± standard error) of a population of 46 clone C males was 751 ± 21.8 μm, and that of a comparable population of 33 clone B males was 531 ± 10.5 μm. Also, the clone C males generally had much more pronounced body-wall outgrowths than clone B males (Fig. 1). The effectiveness of the relatively large size and body-wall-outgrowth development of clone C males in resisting attacks from cannibal females was demonstrated in the feeding experiments. Clone C cruciform predators ingested no clone C males after 167 attempts but did ingest 24 clone B males after 143 attempts ($P = 4 \times 10^{-9}$). Clone C campanulate predators ingested seven clone C males but not before making 49 attacks. Additional observations and experiments showed that clone C campanulates readily attacked and easily ate clone B males and that clone B campanulates ingested 31 male clonemates out of 50 attempts but only two clone C males out of 370 attempts ($P < 1 \times 10^{-9}$).

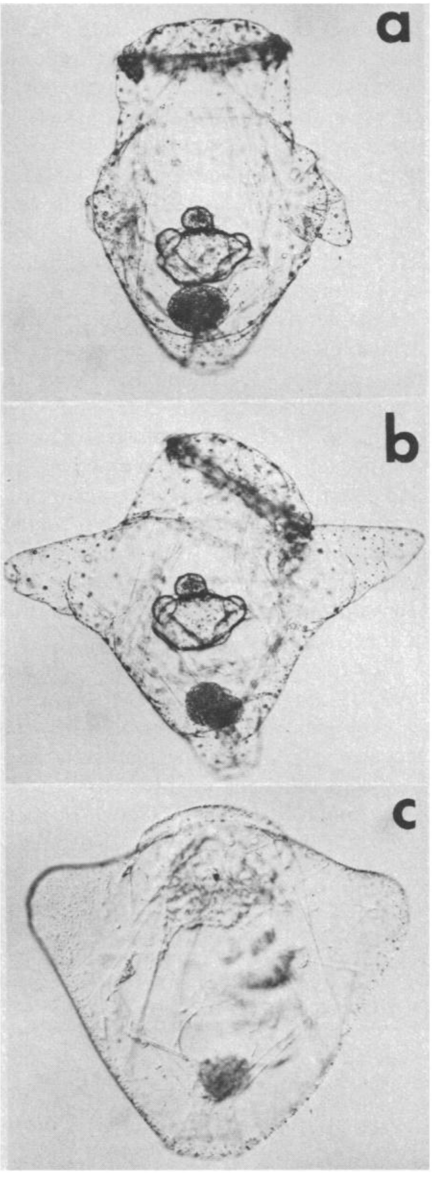

Fig. 1. Live males of *Asplanchna sieboldi*, dorsoventral aspect. Clone C male (870 μm, bright-field optics), showing well-developed body-wall outgrowths withdrawn (a) and extended (b). Clone B male (560 μm, interference-contrast optics), showing poorly developed body-wall outgrowths extended (c).

Therefore, the males of these two clones are protected from cannibalism in different ways. Males of clone B are rarely attacked by campanulate, and possibly cruciform (*11*), clonemates, but have little morphological defense against cannibals which do attack them. In uniclonal populations these males would be almost completely protected from all but very starved cannibalistic females. Also, they may not be attacked by cannibals of other, genetically similar clones. Perhaps partly for this reason, clone B males may have a small body size and only slight body-wall outgrowths. Since males do not feed, all of the energy required for their development and postembryonic life must come from their mothers. Producing small males without elaborate defensive structures might result in more males produced per unit energy cost, thereby increasing the density of males, the probability of male-female contacts, and the production of fertilized, thick-walled resting eggs. Clone B males, however, could be extensively cannibalized by females which did attack them, such as those of clone C. The effectiveness of the clone B type of mechanism for protecting males against cannibalism, therefore, probably depends both on the frequency of encounters with cannibals which do attack them and on the voracity of such cannibals.

Males of clone C are readily attacked by cannibalistic female, especially campanulate, clonemates but have structural adaptations which protect them from being captured. A mechanism by which campanulates avoid attacking male clonemates may not have developed in clone C for several reasons. First, campanulates seem to be rare in this clone (*3*) and so may co-occur with male clonemates infrequently. Second, the great voracity of clone C campanulates might not be compatible with subtle feeding preferences.

It must be emphasized that male anticannibalism devices have been investigated only in these two quite distinct clones. The extent to which the development of the different protective mechanisms may be typical of, and effective within, the respective taxa—probably races or possibly closely related species (*7*)—is not known.

The failure of clone B males to trigger tactile feeding responses in cannibalistic female clonemates appears to be a type of defense against cannibalism not yet reported in other predatory aquatic organisms. It is probably an efficient adaptation because it operates very quickly without involving handling, and possibly damage, of the male by the female. In *Asplanchna*, it may also permit further reduction in male size and structural complexity.

JOHN J. GILBERT
Department of Biological Sciences,
Dartmouth College,
Hanover, New Hampshire 03755

References and Notes

1. J. J. Gilbert and G. A. Thompson, Jr., *Science* **159**, 734 (1968).
2. J. J. Gilbert, *ibid.* **181**, 63 (1973).
3. ______, *Arch. Hydrobiol.* **75**, 442 (1975).
4. ______, *Proc. Natl. Acad. Sci. U.S.A.*, in press.
5. ______, *Oecologia* **13**, 135 (1973).
6. S. H. Hurlbert, M. S. Mulla, H. R. Willson, *Ecol. Monogr.* **42**, 269 (1972).
7. Clones B and C, respectively, were designated as clones 12C1 and 10C6 of *A. sieboldi* by C. W. Birky, Jr., who collected them from a sewage disposal plant in Davis, Calif., in the summer of 1967. However, the females of clone 12C1 resemble those of the questionable species *A. intermedia* in jaw structure [J. J. Gilbert, *Physiol. Zool.* **41**, 14 (1968)]; clone 10C6 is clearly *A. sieboldi* in all respects. Reciprocal matings and cross-fertilizations occur, but the viability of the resting eggs so produced is not known (C. W. Birky, Jr., unpublished results). The clones certainly belong to separate races and perhaps even species.
8. Diets consisted of the ciliate *Paramecium aurelia* with $10^{-7}M$ *d*-α-tocopherol or the rotifer *Brachionus calyciflorus* together with its food organism, *Euglena gracilis*, strain Z.
9. R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969).
10. *HP-65 Stat Pac 1* (Hewlett-Packard, Cupertino, Calif., 1974).
11. The cruciform morphotype of clone B is unstable, rapidly transforming to the campanulate morphotype or to cruciform-campanulate intermediates (*3*), and was not studied.
12. Supported by NSF grant GB-31282, PHS grant 1 R01 HD 08210, and PHS research career development award K04-GM-70557. I thank M. Bean for expert technical assistance and T. M. Frost, J. R. Litton, Jr., P. L. Starkweather, and W. C. Kerfoot for improving the manuscript.

28 June 1976; revised 13 August 1976

Sleep in Mammals: Ecological and Constitutional Correlates

Abstract. *The interrelationships between sleep, ecological, and constitutional variables were assessed statistically for 39 mammalian species. Slow-wave sleep is negatively associated with a factor related to body size, which suggests that large amounts of this sleep phase are disadvantageous in large species. Paradoxical sleep is associated with a factor related to predatory danger, which suggests that large amounts of this sleep phase are disadvantageous in prey species.*

Every mammalian species studied in the laboratory spends at least some time asleep, and some species spend a major portion of their lives in this state (*1*). We may assume that sleep serves some (as yet unknown) biological function, but, if so, why do sleep requirements vary so much from species to species? By correlating sleep habits and other characteristics of species adapted to a wide variety of ecological niches it may be possible to clarify the significance of sleep in the life of mammals.

Comparative sleep data are currently available for fewer than 1 percent of the total species of mammals. However, Zepelin and Rechtschaffen (*2*) computed correlations between some sleep characteristics (such as total sleep time per day) and constitutional variables (such as life-span) and found them to be robust, which suggests that the available data are sufficient to allow at least a preliminary analysis of the biological forces that shape, and are shaped by, sleep.

However, the Zepelin-Rechtschaffen analysis did not include environmental or ecological influences, which may affect sleep (*1, 3, 4*). In one analysis (*4*) species were divided roughly into "good" and "poor" sleepers. Good sleepers sleep at least 8 hours per day, sleep readily in the laboratory, and seem to need a great deal of sleep. Conversely, poor sleepers tend to sleep less and require long periods of adaptation to the laboratory before stable sleep habits are observed. These groups seem ecologically different in two ways. Predators (such as cats) are good sleepers, whereas species subject to heavy predation (such as rabbits) are poor sleepers. Second, species that sleep in reasonably secure places (such as bats) tend to sleep more than species that sleep in the open (such as sheep). We therefore analyzed the interrelationships between sleep, constitutional characteristics, and ecological influences and found that both constitutional and ecological influences are important predictors of the amount and type of sleep obtained by mammals.

This analysis was based on data for 39 species distributed over 13 orders. Incomplete data for 21 additional species were not suitable for the multivariate analyses reported here. The sleep variables we evaluated are the amounts per day of the two qualitatively different stages (*5*): slow-wave sleep (SWS) is characterized by high-amplitude slow waves in the electroencephalogram and by behavioral and autonomic nervous system quiescence; paradoxical sleep

Table 1. Correlation coefficients for sleep, ecological, and constitutional variables (*16*). For all $R > .51, P < .001$. Abbreviations: SWS, slow wave sleep; PS, paradoxical sleep; *L*, life-span; w_b, body weight; w_{br}, brain weight; t_g, gestation time; *P*, predation index; *S*, sleep exposure; *D*, overall danger.

Variables	Correlation coefficients								
	SWS	PS	*L*	w_b	w_{br}	t_g	*P*	*S*	*D*
SWS	1.000	.582	−.377	−.712	−.679	−.589	−.369	−.580	−.542
PS		1.000	−.342	−.370	−.435	−.651	−.536	−.591	−.686
L			1.000	.685	.777	.682	.018	.518	.226
w_b				1.000	.945	.692	.253	.662	.432
w_{br}					1.000	.781	.192	.624	.377
t_g						1.000	.158	.588	.363
P							1.000	.680	.930
S								1.000	.819
D									1.000