observe changes where the environment embraces both harsh and kind habitats. To investigate this the North American marmot offers as good a study animal as has yet ben found. The species are morphologically very alike and occupy a huge range of habitats from the mountain tops above the tree line (Olympic marmot) through the upper forests to the valleys (yellow-bellied marmot) to the plains at sea level (woodchuck). A most interesting gradation in social behaviour has been reported by Barash which, if the interpretations are correct, shows clearly that the quality of social behaviour is correlated with the harshness of the environment (*Science*, **185**, 415; 1974).

Woodchucks living in fields and meadows at low elevation experience a growing season, when their food is rich and abundant, of about 150 days. They are solitary and aggressive. The male–female association last only as long as the brief courtship and mating themselves. Females breed every year and their offspring disperse before the winter. The yellow-bellied marmot lives at elevations where the growing season may last less than 100 days. It is less solitary than the woodchuck but still maintains home areas. They show a greeting behaviour—a pattern never seen in woodchucks—and greet their neighbours two or three times daily. The Olympic marmot is restricted to the treeless alpine meadows of Olympic National Park, Washington, where the growing season may be as short as 40 days. These are highly gregarious animals which live in well organised colonies of adults, 2-year-olds, yearlings and infants. They do not protect home areas and wander about the colony without fear of attack. Their level of aggression is low and in consequence greet one another about ten times as frequently as their yellow-bellied cousins. Females breed every other year and youngsters do not disperse until they are 2 years old. By the time they reach this age they weigh 70% of the adult weight. In comparison woodchucks (weighing 80% of adult weight) disperse before their first winter.

The important thing for a species is to leave the maximum number of surviving offspring that the habitat will carry. Because of the varying durations of growing seasons encountered by marmots the optimum age for dispersal varies between a few months and 2 years. Barash demonstrates that the environment dictates when dispersal takes place through the effect of growth rate on aggressiveness. If overwinter mortality has been high and the population needs replenishing, the level of aggression is a little lower and a higher proportion of the dispersers remain, and *vice versa*—a very clear example of adaptive social behaviour.

Several factors may complicate Barash's simple interpretation—for example, female Olympic marmots breed once in 2 years while the other species bred annually. The reproductive physiology and feeding ecology of a species play a fundamental part in moulding the shape of the behavioural fine tuning. Barash's work demonstrates beautifully that the barrier between ethology and ecology is more imagined than real.

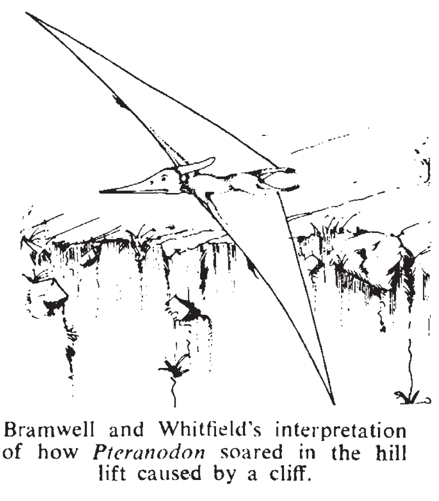
Prehistoric gliders

from a Correspondent

In a study of the biomechanics of *Pteranodon*, Bramwell and Whitfield discuss the structure and aerodynamics of the largest flying animal to have existed. As *Pteranodon* represented the end product of pterosaur evolution it was likely to show a high degree of structural and aerodynamic refinement and this has been largely confirmed *within this study* (*Phil. Trans. R. Soc.*, **B267**, 503–592; 1974).

Any such study as this is based upon conjecture—indeed herein lies one of its fascinations—but the authors have minimised uncertainty in this respect by utilising an interdisciplinary approach, combining both engineering and palaeontology to formulate conclusions. The application of engineering to an extinct animal is obviously extremely difficult, particularly as parts of the fossil animal were missing. The authors have, however, used the best data available and where their conclusions are open to doubt this in no way infers a criticism of this study, but of the lack of information particularly within the field of low speed aerodynamics.

From available fossil and estimated sizes the strength of the bones in the wing spars has been calculated. The general factor of safety is approximately 5 which is a reasonable value for a flying animal with the assumed flight activities of *Pteranodon*. The most surprising feature of the structure is a factor of safety of only 2 for the humerus. It is possible that the assumed strength values for this bone were incorrect and the authors have considered this as one possibility by suggesting that a stronger, more brittle bone material was practical. They also put forward a more feasible explanation in that part of the loads could be taken by some of the flight muscles being inserted well out along the humerus.



Bramwell and Whitfield's interpretation of how *Pteranodon* soared in the hill lift caused by a cliff.

From tests in a wind tunnel Bramwell and Whitfield provide a new explanation of the large crest on the animal's head. This structure had previously been thought to have the effect of a rudder or steering device but these authors clearly show that it was a weight-saving device; by balancing the aerodynamic loads on the beak it could reduce the required neck muscles and thereby save weight.

The aerodynamic characteristics of the wing were based on the use of data for the Gottingen 417a curved plate as being the nearest to the *Pteranodon* wing section. There is a discrepancy between the drag values of the Gottingen 417a aerofoil section as presented by Schmitz and that presented in Figure 44 by Bramwell and Whitfield, but it is obvious that these authors have used the data from Schmitz for all their performance estimations.

It is unfortunate that there are no more recent data than those for the 417a section nor any more appropriate aerofoil section on which to base the estimations of *Pteranodon*'s performance. From a polar curve of *Pteranodon* the best flying speed was about 8 m s^{-1} with a minimum sinking speed of 0.43 m s^{-1}. The highest useful flying speed was about 14 m s^{-1}. These estimates of performance are realistic as any small discrepancies in the assumed wing drag characteristics are unlikely to have a profound effect on the overall lift/drag ratio.

A comparison between the performances of *Pteranodon*, an albatross and a modern high performance glider shows that *Pteranodon* was a very efficient glider with a sinking speed of about half that of the other two. From estimates of power required it seems that *Pteranodon* was also just capable of powered flight for short durations.

Bramwell and Whitfield conclude that *Pteranodon* was primarily a glider that utilised sea thermals for lift while searching for food. Although dynamic soaring is used by the albatross to sustain flight over the sea, the authors show that *Pteranodon* was unlikely to utilise this form of lift because of its low flying speed and the critical conditions for the required wind gradient.