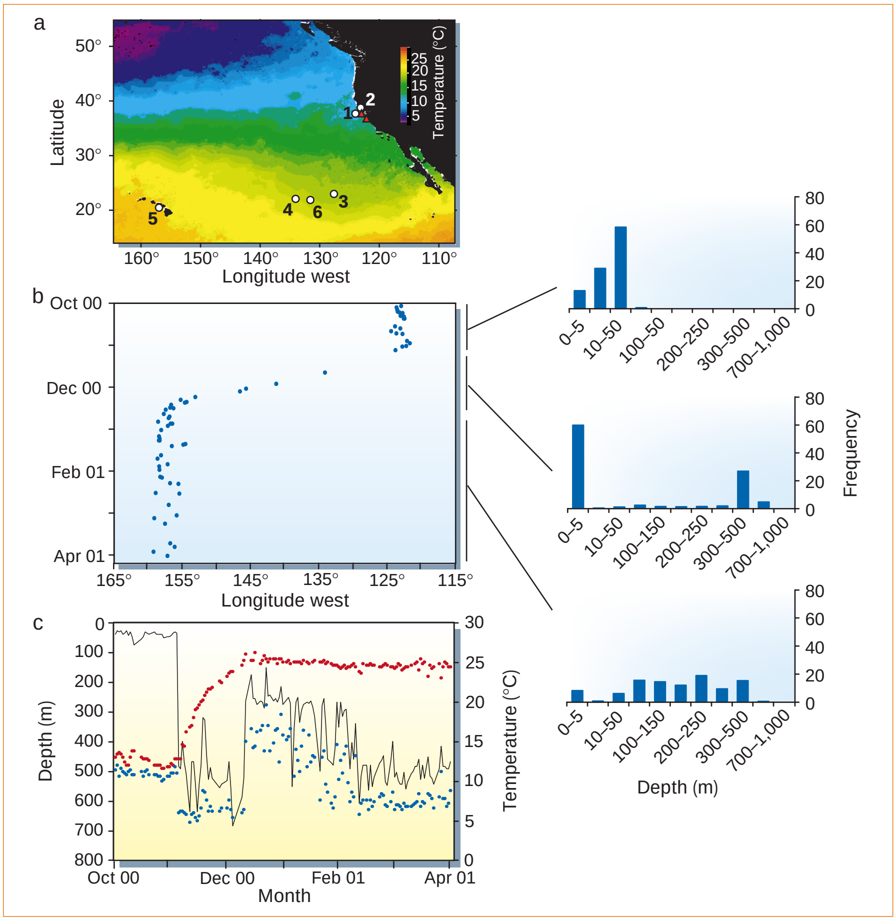

Figure 1 Movements, diving and temperature preference of white sharks. **a,** Deployment (red triangles) and end-point locations (white circles) for sharks tagged with pop-up satellite archival tags. Deployment dates are given first, followed by pop-off dates. 1, 19 October 1999; 2 November 1999. 2, 30 October 1999; 25 November 1999. 3, 16 October 2000; 19 February 2001. 4, 10 December 2000; 9 April 2001. 5, 16 October 2000; 16 April 2001. 6, 5 November 2000; 8 May 2001. Sea-surface-temperature image is a weekly composite for 21–28 February 2001. **b,** Longitude and depth distribution of shark 5 over the course of its 182-day tracking period. **c,** Data for shark 5 over the course of the tracking period: black line, maximum daily depth; red points, sea-surface temperature; blue points, minimum daily temperatures. Coastal residence is indicated by shallow maximum depths (which correspond to the shark's position over a continental shelf), low sea-surface temperature and narrow ambient temperature range.

Kahoolawe; three others (sharks 3, 4 and 6) moved to a region of the subtropical eastern Pacific (Fig. 1a). All four sharks showed a period of bimodal preference for depths of 0–5 m and 300–500 m, spending up to 90% of the day in these depth ranges and little time at intermediate depths (Fig. 1b shows representative data for shark 5). As the sharks moved southwest, they increased their maximum diving activity and experienced a broader range of ambient temperatures. Sea-surface temperatures rose to 20–26 °C, and the minimum temperatures at maximum depths (650–680 m) dropped to 4.8 °C (Fig. 1c), suggesting that white sharks can tolerate a broad temperature range.

The shark that travelled to Hawaii crossed 32° of longitude in 40 days at a minimum velocity of 71 km per day (Fig. 1b). Although sightings of white sharks in Hawaiian waters are rare[12], this individual remained in the vicinity for almost 4 months, primarily staying between the surface and 300 m throughout this period (Fig. 1b).

These data provide the most extensive record so far of the ecological niche of white sharks. Our results indicate that their range is more pelagic than was previously thought, comprising an inshore continental-shelf phase as well as extensive oceanic travel. The offshore phase lasted for at least 5 months, suggesting that it is an important period in the life history of white sharks in the North Pacific. It is unclear whether these offshore movements, which include extensive deep dives, represent feeding or breeding migrations. Increased tracking using electronic tagging should provide more data about the movement patterns, habitat usage and potential fishery interactions of white sharks, as well as critical information needed for the conservation of this species.

Andre M. Boustany*, Scott F. Davis†,
Peter Pyle‡, Scot D. Anderson‡,
Burney J. Le Boeuf†, Barbara A. Block*
**Tuna Research and Conservation Center,*
Stanford University and Monterey Bay Aquarium,
Hopkins Marine Station, Pacific Grove,
California 93950, USA
e-mail: bblock@stanford.edu
†Institute of Marine Sciences, University of
California at Santa Cruz, Santa Cruz,
California 95064, USA
‡Point Reyes Bird Observatory, Stinson Beach,
California 94970, USA

1. Metcalfe, J. D. & Arnold, G. P. *Nature* **387,** 665–666 (1997).
2. Block, B. A., Dewar, H., Farwell, C. & Prince, E. D. *Proc. Natl Acad. Sci. USA* **95,** 9384–9389 (1998).
3. Block, B. A. *et al. Science* **293,** 1310–1314 (2001).
4. Eckert, S. A. & Stewart, B. *Environ. Biol. Fish.* **60,** 299–308 (2000).
5. Carey, F. G. & Teal, J. M. *Comp. Biochem. Physiol.* **28,** 199–204 (1969).
6. Compagno, L. J. V. *FAO Fish. Synop.* **125,** 1–249 (1984).
7. Klimley, A. P. *Mem. South. Calif. Acad. Sci.* **9,** 15–40 (1985).
8. Goldman, K. J., Anderson, S. D., McCosker, J. E. & Klimley, A. P. in *Great White Sharks: The Biology of* Carcharodon carcharias (eds Klimley, A. P. & Ainley, D. G.) 111–120 (Academic, San Diego, 1996).
9. Klimley, A. P. *et al. Mar. Biol.* **138,** 617–636 (2001).
10. Hill, R. D. in *Elephant Seals: Population Ecology, Behavior, and Physiology* (eds LeBoeuf, B. J. & Laws, R. M.) 227–236 (Univ. California Press, Berkeley, 1994).
11. Welch, D. W. & Everson, J. P. *Can. J. Fish. Aquat. Sci.* **56,** 1317–1327 (1999).
12. Taylor, L. *Mem. South. Calif. Acad. Sci.* **9,** 41–48 (1985).

Supplementary information accompanies this communication on *Nature*'s website (www.nature.com).

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Carnivorous plants

Mass march of termites into the deadly trap

Carnivorous pitcher plants of the genus *Nepenthes* are not usually very selective about their prey, catching anything that is careless enough to walk on their slippery peristome, but *Nepenthes albomarginata* is an exception. We show here that this plant uses a fringe of edible white hairs to lure and then trap its prey, which consists exclusively of termites in enormous numbers. This singular feature accounts for the specialization of *N. albo-*

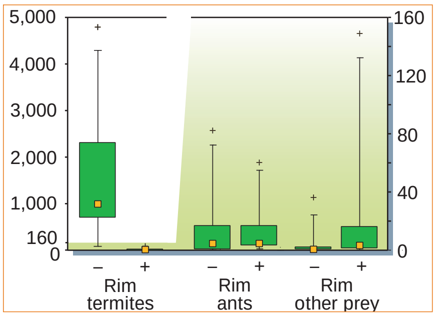

Figure 1 Comparison of prey composition for pitchers with intact and with grazed-down rim hairs (box plot; rim condition: minus sign, grazed down; plus sign, intact). The prey groups 'ants' and 'other prey' (right) are presented on an extended scale. For statistical analysis, we used the non-parametric Mann–Whitney *U*-test. There is a significant difference in the number of termites ($P > 0.02$), but no significant difference for the prey-group ants. The difference in the number of the group 'other prey' was significant ($P > 0.02$) but in our opinion this was too heterogeneous to allow any conclusions to be drawn. Details are available from the authors. Plus signs, maximum values; hollow squares, medians; error bars, limits; green boxes, 25th to 75th percentiles.

marginata for one prey taxon, unique so far among carnivorous plants.

The main attractant for insect prey (ants are most common[1–3]) in most *Nepenthes* species is its nectar, which may be associated with a distinctive pitcher colour and smell[1]. But *N. albomarginata* T. LOBB ex LINDL works differently. If no termites are present, the harvest diversity looks much the same, except that the catch is even poorer than in neighbouring pitcher plants of other species: a few dozen ants, beetles or flies caught over the six-month lifespan of the pitcher. However, termites have frequently been found in *N. albomarginata* pitchers, a feature seldom, if ever, associated with other species[3–5].

We studied *N. albomarginata* in Brunei and usually found thousands of termites trapped in a single pitcher (Fig. 1). All termites in one pitcher belonged to the same species and were in the same state of decomposition, suggesting that they were caught over a short period. We found three termite genera, all belonging to the subfamily Nasutitermitinae, with one genus (*Hospitalitermes*) predominating. The feeding by this termite on live fungal and algal tissue and its habit of foraging over ground in mass columns are extraordinary among termites.

N. albomarginata has a unique morphological feature, a rim of living white trichomes directly below the peristome (Fig. 2). This had not previously been associated with the plants' feeding habits until one of us (D.J.M.) noticed that the rim's hairs were missing from pitchers that had caught termites. A comparison of large numbers of pitchers over a prolonged period confirmed the correlation. For several days, nothing would happen, then — after a single night — pitchers would fill with termites and their rim hairs would disappear.

To investigate this, we placed fresh intact pitchers, together with pitchers with their white rims removed, near to the head of foraging columns of the termite *Hospitalitermes bicolor*. When single leading workers came into direct contact with the white rim hairs, they turned back to the column and recruited their nestmates, which began grazing on the rim and forming food pellets from the white trichomes (Fig. 2). While doing this, the termites fell into the pitchers in their masses, workers and accompanying soldiers alike. Once in the pitcher, they were unable to grip the peristome to climb out. Observation of one grazing *H. bicolor* column revealed that up to 22 individuals per minute were falling into the pitchers, but the capture rate could easily exceed this for denser columns. Outside the pitcher traps, the termites at the column head displayed typical foraging and recruitment behaviour[6,7]. After about an hour, the hairs were all gone and the pitcher was evidently no longer attractive to termites (and was filled with termites trying to escape).

Figure 2 A pitcher of *Nepenthes albomarginata* being visited by termites. Nasuti termite workers and soldiers are harvesting the white rim hairs, which may mimic the appearance of termites' food. As the insects lose their grip on the peristome, hundreds or even thousands fall into the pitcher, where they are trapped.

We do not know how the trichomes lure termites onto the plant. No long-range olfactory attraction could be detected during our experiments; all contacts seemed to happen by chance, with termites often missing pitchers less than 1 cm away from them.

Prey specialization has been proposed for some *Nepenthes* species[3] but, to our knowledge, *N. albomarginata* is the first example of a carnivorous plant in which this has been confirmed and functionally described, as well as being the only species to offer its tissue as a bait.

Marlis A. Merbach*, Dennis J. Merbach*, Ulrich Maschwitz*, Webber E. Booth†, Brigitte Fiala‡, Georg Zizka§

**Fachbereich Biologie, Zoologisches Institut, Johann Wolfgang Goethe-Universität, Frankfurt am Main, Postfach 111932, 60054 Frankfurt, Germany*
e-mail: merbach@zoology.uni-frankfurt.de
†*Biology Department, Universiti Brunei Darussalam, Brunei Darussalam, Borneo*
‡*Universität Würzburg, Zoologie III, Biozentrum, Am Hubland, 97074 Würzburg, Germany*
§*Botanik/Paläobotanik, Johann Wolfgang Goethe-Universität und Forschungsinstitut Senckenberg, 60325 Frankfurt am Main, Germany*

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1. Moran, J. A. *J. Ecol.* **84,** 515–525 (1996).
2. Moran, J. A., Booth, W. E. & Charles, J. K. *Ann. Bot.* **83,** 521–528 (1999).
3. Kato, M., Hotta, M., Tamin, R. & Itino, T. *Trop. Zool.* **6,** 11–25 (1993).
4. Clarke, C. M. Nepenthes *of Borneo* (Natural History Publications (Borneo), Kota Kinabalu, Sabah, Malaysia, 1997).
5. Adam-Jumaat, H. *Pertanika J. Trop. Agric. Sci.* **20,** 121–134 (1997).
6. Jones, D. T. & Gathorne-Hardy, F. *Insectes Soc.* **42,** 359–369 (1995).
7. Miura, T. & Matsumoto, T. *Insectes Soc.* **44,** 267–275 (1998).

Competing financial interests: declared none.

COMMUNICATIONS ARISING

Geoarchaeology

Did Nile flooding sink two ancient cities?

The discovery of the two cities of Herakleion and East Canopus under the waters of the Bay of Abu Qir (east of Alexandria, Egypt) stirred worldwide attention when it was first announced in the summer of 2000. Their disappearance some 1,250 years ago has been ascribed by Stanley, Goddio and Schnepp[1] to a strong Nile flood that caused riverbank failure and the destruction of the two cities, rather than to the action of earthquakes, as was first proposed when the ruins were discovered[2,3]. But I believe that this interpretation is flawed, because no flood could have reached the Abu Qir Bay at the time of the disappearance of the two cities, as the Canopic branch of the Nile, along whose banks they were situated, had dried to a trickle more than 200 years earlier.

This consideration seems to have been overlooked by Stanley *et al.*, who assume that the Canopic remained active until late in the first millennium. Toussoun, who is cited as the main reference for that assumption, is clear on this point: on pages 195–196 of his work[4], he gives evidence that the Canopic silted up gradually during the fifth century and that it stopped flowing into the bay long before the Arab armies reached Alexandria; he found no mention of it in any of the accounts of the Arab historians.

The radiocarbon ages given by Stanley *et al.* for the mud "immediately beneath the ruins" confirm this view: none is younger than AD 322. I know of no mention of this branch of the delta past the fifth century AD, neither is there any evidence of it on the maps prepared by Napoleon's savants in the eighteenth century.

Even if we accept the authors' assumption that the Canopic was still active at the time of the disappearance of Eastern Canopus and Herakleion, it is unlikely that the destruction of these two cities would have been brought about so suddenly. There is no mention of such a cataclysmic event in any of the texts written around this period, nor of the destruction of any other city along the length of the Nile.

The flood in AD 741/742 was not likely to have been dangerous or destructive. For those who know the Nile and the history of its use, floods associated with higher water levels than normal were welcome events. Before the system of perennial irrigation was introduced in the nineteenth century, the lowlands of the flood plain of the river were left fallow during the flood season in readiness to receive the waters of the flood and to give rise to a larger tract of arable land.

The disastrous floods dreaded in those